ECOLOGICAL MONOGRAPHS

VOLUME 14 JANUARY, 1944 NUMBER 1

EFFECTS OF DROUGHT, DUST, AND INTENSITY OF GRAZING ON COVER AND YIELD OF SHORT-GRASS PASTURES[1]

F. W. ALBERTSON
Fort Hays Kansas State College

and

J. E. WEAVER
University of Nebraska

[1] This study was made with the aid of a grant from the Penrose Fund of the American Philosophical Society.

TABLE OF CONTENTS

	PAGE
INTRODUCTION	3
METHOD OF STUDY	4
ENVIRONMENTAL CONDITIONS	5
Precipitation	6
Soil Moisture	6
Temperature, Evaporation, and Wind	8
BASAL COVER AND COMPOSITION OF VEGETATION	9
Hays Pastures	9
Ness City Pastures	11
Quinter Pastures	14
Dighton Pastures	15
Discussion	17
ANNUAL YIELD OF NATIVE GRASSES AND WEEDS	18
Hays Pastures	18
Ness City Pastures	20
Quinter Pastures	20
Dighton Pastures	21
Discussion	22
MONTHLY YIELD OF NATIVE GRASSES	23
Discussion	24
EFFECT OF DIFFERENT INTENSITIES OF CLIPPING ON YIELD	25
Discussion	26
SUMMARY	27
LITERATURE CITED	29

EFFECTS OF DROUGHT, DUST, AND INTENSITY OF GRAZING ON COVER AND YIELD OF SHORT-GRASS PASTURES

INTRODUCTION

The vast range lands of western Kansas occupy approximately one half of that area. They are now recovering from the terrible destruction wrought by overgrazing, drought, and dust-burial during the past decade. Since grass is man's most powerful ally in soil and water conservation, since pastures are tremendously important as the cheapest and most satisfactory feed for cattle, and since the recovery of the western range is not only an economic problem of great importance but a phenomenon of outstanding ecological interest, the redevelopment of the plant cover warrants careful investigation.

The pastures of western Kansas occupy a diversified topography and vary considerably in composition of vegetation. Those on the eastern edge of the area are a part of the mixed prairie association in which certain postclimax tall grasses extend westward in long arms and occupy the more moist soil, especially in ravines, and often intermix with mid grasses on steep hillsides, frequently where the soil is shallow and rocks outcrop. The short-grass disclimax, resulting from long continued grazing of the mixed prairie, occupies the level and gently rolling lands and extends westward over a vast area with decreasing precipitation. Since this blue grama *(Bouteloua gracilis)*-buffalo grass *(Buchloe dactyloides)* type is of the greatest extent and importance, it has received major consideration in this investigation. The pastures vary in size from 20 to 40 acres on farms where cultivated land is extensive to several thousand acres on rough land where growing cultivated crops is only incidental to livestock production. In many localities the income from the farm is almost entirely dependent upon livestock (Fig. 1).

An understanding of present conditions can be had only by a knowledge of past treatment of the

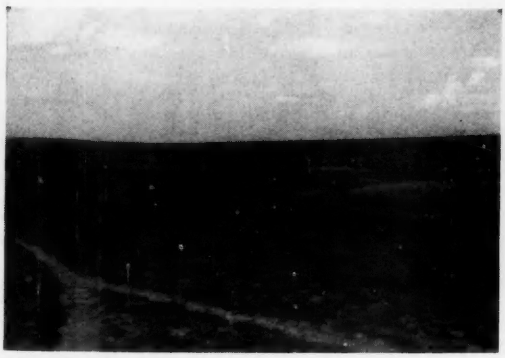

FIG. 1. Range land typical of western Kansas where the short grass furnishes most of the forage for livestock. August, 1942.

ranges. High wind movement was common throughout the drought period and especially severe during the spring of 1935. Soil which was pulverized by excessive cultivation was carried as dust in large quantities from cultivated fields and deposited in layers or drifts on the drought-stricken prairie plants (Fig. 2). The cover of native vegetation was thus greatly reduced, in fact, the grasses were almost or completely annihilated over vast areas of range land.

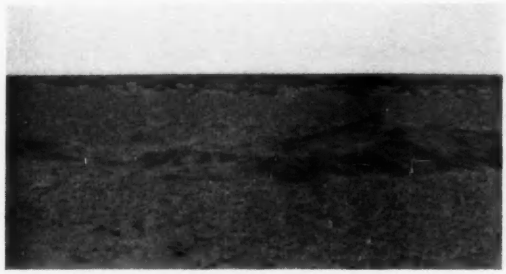

FIG. 2. Surface soil carried by wind from adjacent cultivated land and deposited in layers and drifts on a sparse, weakened vegetation. Lakin, Kan. July, 1939.

Planted crops failed to grow because of deficient moisture. This compelled the rancher to increase the usual length of the grazing season as well as the intensity of range utilization. This extreme overgrazing was responsible for further decline in the amount of original plant cover. The soil when devoid of native vegetation was often populated by numerous weedy annuals (Fig. 3). As a result, many farmers were confronted with the problem of increased losses in livestock due to the poisoning effect of various noxious weeds.

FIG. 3. Large Russian thistles forming a new cover on the drought-swept prairie. Usually the dead crowns of native grasses (foreground) furnished the only evidence that the area was once clothed with a dense cover of short grasses. This is typical of hundreds of ranges in western Kansas. Photo August, 1939.

The prairie soil was bared by adverse environmental conditions and became extremely susceptible to wind erosion. It was the source of dust for further great storms which greatly damaged the ranges. When pastures were placed under the stress of these unfavorable environmental conditions it became evident that in those where good management had been practiced the original plant population suffered far less than where overgrazing or overgrazing with intense dusting had occurred. This investigation was initiated to determine the effect of drought, different intensities of grazing, and degrees of dusting from adjacent cultivated fields upon the basal cover and yield of the native vegetation.

METHOD OF STUDY

The plan of the investigation was to select a series of pastures which had been detrimentally affected by past usage or environment in different degrees and to measure the nature and rate of recovery under protection. Increase in basal area, amount of the various species concerned, and dry weight of forage produced were the chief criteria used in measuring recovery. This included, of course, a consideration of the environmental conditions of growth. Effects of different intensities of clipping were also ascertained as well as the monthly yield.

Basal area gives a good picture of the structure of a type of vegetation. When used in permanent quadrats, the increase or decrease in the abundance of individual species due to succession or different treaments can be followed accurately. Although the percentage results are not a sensitive measure of the change in yield, they definitely reflect any change in the nature of the plant cover (Savage 1937; Weaver & Albertson 1936). Dry weight of plants is one of the best quantitative characteristics of vegetation (Hanson 1938), and increase in dry weight is the best measure of growth (West, Briggs, & Kidd 1920). When basal area and dry weight are combined in a study of recovery of sod- and bunch-forming grasses a rather clear picture of development should be obtained.

The clip quadrat has been widely used by numerous American investigators in obtaining yields (Sampson 1914; Sarvis 1923; Taylor & Loftfield 1924; Canfield 1939; Hein & Henson 1942; and others). Although clipping studies serve as a valuable supplement to grazing experiments, they differ in several respects from actual grazing. The chief differences have been pointed out by Culley, Campbell, and Canfield (1933) and Donald (1941). But despite these differences clip quadrats are invaluable and are widely used wherever quantitative ecological studies in grassland are pursued (West 1936).

Four pastures, representing various stages in range deterioration, were selected near each of four stations —Hays, Ness City, Quinter, and Dighton, Kansas. In addition, a prairie was selected near Phillipsburg, Kansas. Hays is in Ellis County and about 160 miles from the western state boundary. Phillipsburg lies 65 miles directly north of Hays and is in the northern tier of counties. Quinter is 50 miles west and north of Hays and Ness City and Dighton are 60 and 100 miles, respectively, southwest. All of these extensive ranges are in the mixed prairie association, and all but the prairie at Phillipsburg are portions of a great grazing disclimax. At Phillipsburg the vegetation has changed from mixed prairie to an open stand of short grass solely as a result of drought and coverage by dust.

The pastures at each station, except Phillipsburg, were of four different classes as follows:

Class 1. Lightly grazed and lightly dusted.
Class 2. Heavily grazed and lightly dusted.
Class 3. Lightly grazed but heavily dusted.
Class 4. Both heavily grazed and heavily dusted.

Intensity of grazing in the class 1 and 2 pastures at Hays had been about 1 animal unit for each 20 acres, and in other class 1 and 2 pastures about 1 animal unit for each 20 to 30 acres, although the use records at Quinter are incomplete. Class 3 pastures were similar to class 1 before the heavy dusting. Moreover, during years of poor productivity these pastures had been withheld from grazing. The heavily grazed class 2 and class 4 pastures had been stocked at the rate of 1 animal unit for each 8 to 12 acres, and grazing was more or less continuous regardless of precipitation.

The class 1 pasture at each station represented the best conditions found in that vicinity. Grazing was light and frequently deferred until about August 1, a practice common among the best cattle producers even before the dry cycle. Drought damage under this type of utilization was reduced to a minimum. These pastures were commonly located at some distance from cultivated fields or if in close proximity to them judicious soil management had been practiced to prevent dust blowing. Thus, coverage by dust, locally known as dusting, was almost negligible (Fig. 4A). At Phillipsburg the vegetation was identical with that of a class 1 pasture.

Class 2 pastures were subjected to considerably heavier grazing than were those of the first class. Dusting, however, was usually scarcely more intense (Fig. 4B).

In class 3 pastures grazing was so light that it did not reduce the plant cover. Considerable damage, however, had resulted from dust blown from adjacent cultivated fields (Fig. 4C). This class is placed third since heavy dusting is even more injurious to short grass than heavy grazing.

Class 4 pastures were the poorest that could be found in each locality. Grazing and dusting had usually been so severe that little or none of the original vegetation remained (Fig. 4D).

Twenty meter quadrats, arranged in groups of four for convenience of examination, were staked out in each pasture and clipped annually (Fig. 5). Approximately 16 other similar quadrats in each exclosure were included in 1941 to secure data on the monthly yield in relation to intensity of grazing as simulated by frequent clipping. Livestock were ex-

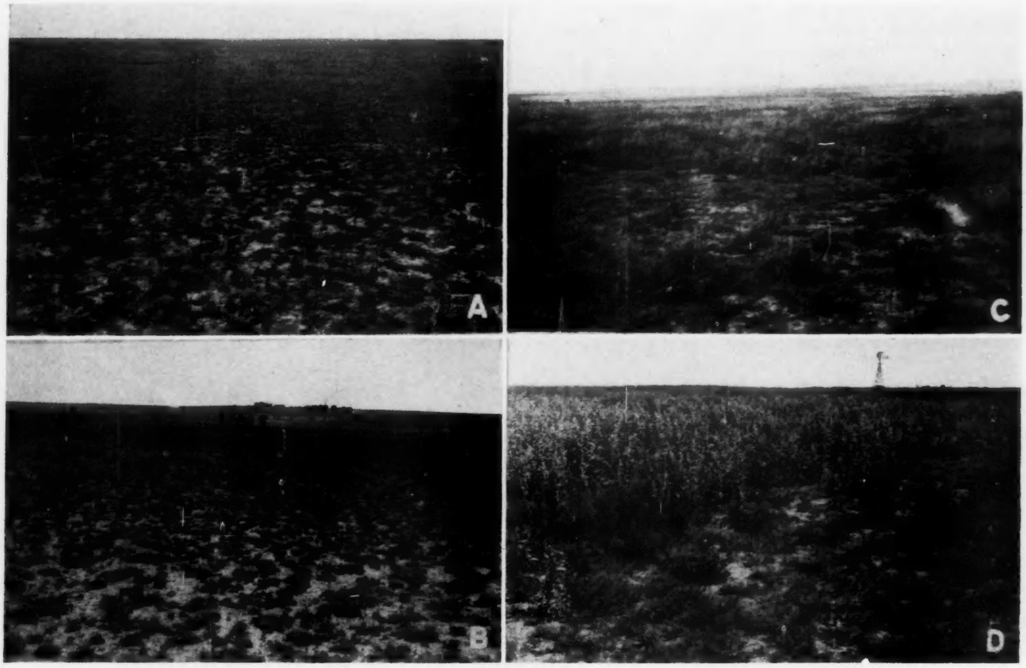

FIG. 4. A. Typical view of a class 1 pasture where the open cover remained intact throughout most of the drought. Dighton, Kan. September, 1940. B. A class 2 pasture with typical open cover. In early spring such ranges were usually infested with *Lepidium densiflorum*, *Lappula occidentalis*, and other annual weeds. August, 1940. C. View of a class 3 pasture near Ness City, Kan., where the original amount of cover and its composition had been greatly modified. Many weeds such as *Salsola pestifer* were scattered over the prairie. September, 1940. D. An overgrazed pasture heavily dusted in 1935, near Dighton. Most of the original cover died and has been replaced by *Chenopodium album*, *Helianthus annuus*, *Amaranthus retroflexus*, and other weeds. June, 1940.

cluded from these areas by means of barbed wire fences. All forage was clipped monthly to within one half inch of the surface of the soil except that harvested only at the end of the summer. The forage was separated into short grass, mid grass, native forbs, and weeds and placed in paper bags. It was air-dried and weighed to the nearest tenth gram. Yields, exclusive of native forbs, were expressed in pounds per acre. Native forbs were not included

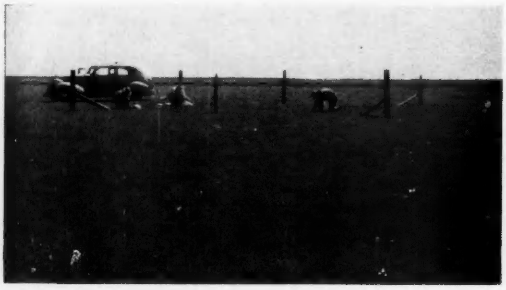

FIG. 5. View of an exclosure in class 1 pasture near Dighton. The corners of each quadrat were marked permanently with stakes. A thick growth of *Lepidium densiflorum* gives the appearance of a good stand of grass.

since they were absent over 60 percent of the area and were inconsequential in the remainder.

The exclosures and the surrounding pastures were examined monthly. Approximately half of the quadrats were charted (that is, the basal area mapped at a height of one half inch) each fall by means of a pantograph. In charting, only places without cover of native perennial grasses and larger than .8 inch in diameter were considered bare. The percentage of basal cover for each species in each quadrat was obtained by use of a planimeter or by superimposing circles of known area inscribed on tracing paper upon those of the charted quadrat sheet.

Water content of soil was determined at regular intervals throughout the growing seasons of 1940 and 1941. Records of precipitation and temperature were secured from the United States Weather Bureau which has an observer at each of the stations.

ENVIRONMENTAL CONDITIONS

The climate of the mixed prairie region is characterized by great fluctuations in the amount and time of precipitation, temperature, humidity, and wind movement. There are often long periods during the growing season with little or no rainfall when

temperature and wind movement are high and the relative humidity and available soil moisture extremely low. The years 1940 and 1941 immediately followed a seven-year period of the most intense drought ever recorded. The accumulated deficits in precipitation at the five stations varied from 24.4 inches at Quinter to 43.1 inches at Phillipsburg. During the drought, the annual precipitation at any of the five stations exceeded the normal only twice; the soil became exceedingly dry to a depth of five feet, and vegetation was greatly damaged (Weaver & Albertson 1940; Albertson & Weaver 1942).

PRECIPITATION

Low precipitation in 1939 had a pronounced carry-over effect upon the native vegetation and for that reason it as well as the precipitation during the experiment must be considered. Total annual precipitation at Phillipsburg in 1939 was nearly 10 inches below the normal of 23 inches. The next greatest deficit was 8.3 inches at Dighton. Precipitation deficits of 7.8, 7.0, and 5.0 inches, respectively, occurred at Hays, Ness City, and Quinter. Precipitation during the growing season (except June and August at Hays and August at Quinter) was below normal and usually far below for all of the summer months at all of the stations. The season was especially unfavorable to growth because of the long period of drought in autumn. It was during this time that the vegetation acquired the bluish-gray cast common to the short grasses after their death.

Precipitation during 1940 was above normal at Ness City and approximately normal at Hays (Fig. 6). It was somewhat below normal at Quinter and Dighton, but about 6 inches below at Phillipsburg. This growing season showed much improvement over that of 1939 (Figs. 6 and 7). Precipitation exceeded the normal, however, only about one third of the time. Rainfall for April and June was below normal at all five stations. It was normal or above at all stations during August, but during the remaining three months it was above normal at some stations and below at others.

The year 1941 showed still greater improvement in amount and distribution of precipitation. Rainfall was above normal more than half the time from April to September. It was much above normal at all stations during April and June; June, in particular, was an unusually wet month, at most stations the rainfall was at least twice normal. For example, it was 8.7 inches at Phillipsburg and 10.7 at Quinter. The rainfall for the remaining four summer months was somewhat erratic. At some stations it was much above normal, at others considerably below. At Hays, for example, rainfall during May was about .5 inch below normal, while at Dighton it was more than twice normal. Such differences had a significant effect upon the amount of soil moisture and the yield of forage at the two stations.

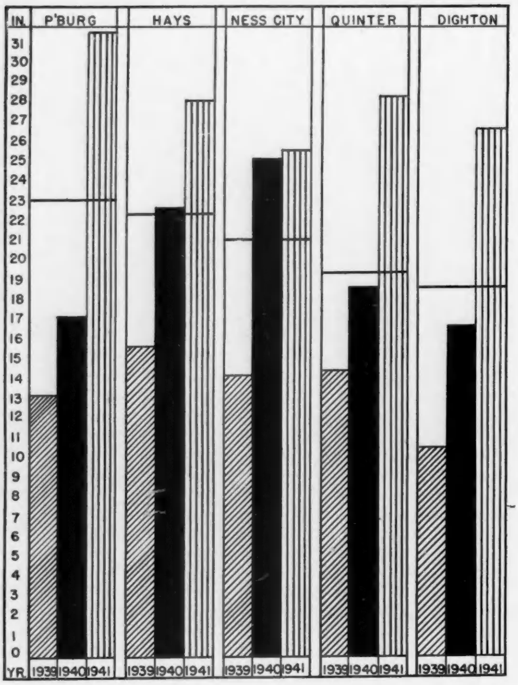

FIG. 6. Annual precipitation at the several stations. Normal precipitation is shown by the heavy horizontal lines.

SOIL MOISTURE

Determinations of water content of soil were made to a depth of 5 feet each month during the growing seasons of 1939, 1940, and 1941 at Phillipsburg, Hays, and Dighton. Total water content of soil minus the hygroscopic coefficient (which was determined for each soil depth at each station) is designated as water available for growth. The hygroscopic coefficients of these silt-loam or very fine sandy-loam soils ranged between 9.0 and 13.9 percent.

At Phillipsburg, the soil was moist to a depth of 2 feet in April, 1939, but this amount was soon reduced by vigorous absorption by the rapidly growing vegetation (Fig. 8). The 0.8 inch of rainfall during May was not enough to supply the demands for plant growth, and when soil samples were taken at the close of the month no moisture was available to a depth of 4 feet and less than 2 percent occurred in the fifth foot. Showers amounting to 3.6 inches during June but only 0.9 inch in July resulted in less than 5 percent available moisture in the surface foot and none below that depth. Moisture was further depleted during August. Continued drought during the fall resulted in the soil becoming so dry that much of the native vegetation died.

Winter snows and spring rains resulted in moist soil to a depth of a foot by April, 1940. This was soon exhausted and there was no available water on

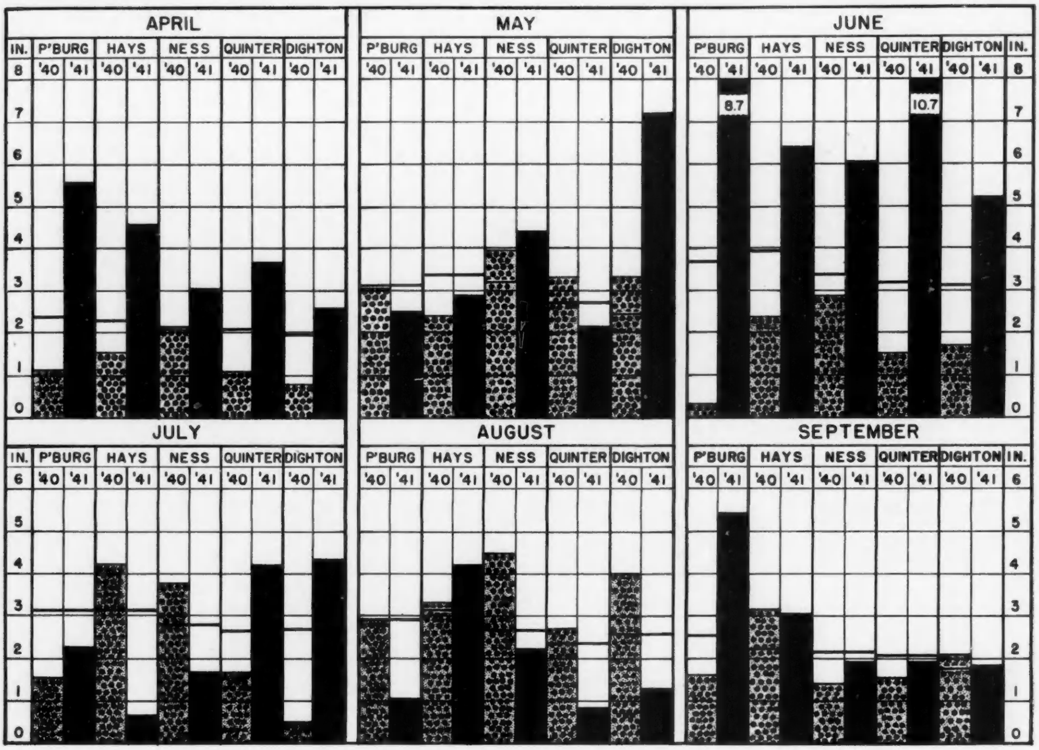

FIG. 7. Monthly precipitation (April to September inclusive) at each station in 1940 and 1941. The heavy horizontal lines indicate normal rainfall.

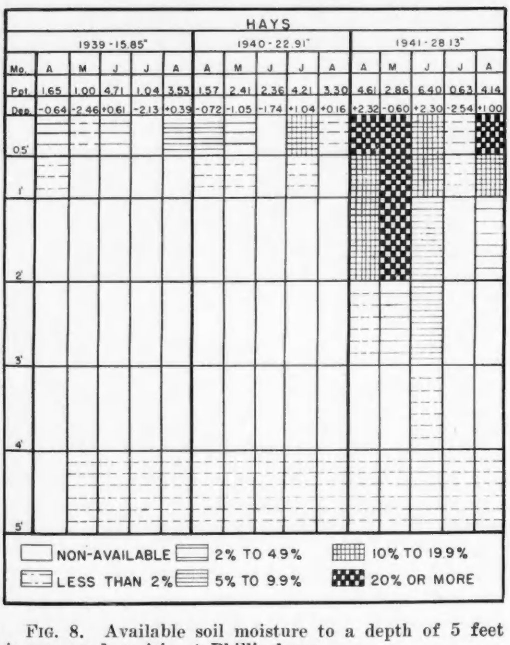

FIG. 8. Available soil moisture to a depth of 5 feet in ungrazed prairie at Phillipsburg.

the dates of sampling during the remainder of the growing season. It is probable, however, that some moisture was available in the surface soil at intervals between the samplings.

In April, 1941, available moisture extended to a depth of 2 feet. Moist soil occurred to 4 feet on May 31, and by June 30 more than 20 percent moisture was available to a depth of 2 feet and from 5 to 15 to a depth of 5 feet. Moderate drought occurred in the upper soil during July but water was available below 12 inches. Abundant water for plant growth was found in the soil during August. The contrast of the favorable conditions of growth in 1941 to the extremely unfavorable ones in 1940 is very striking.

At Hays, the soil was extremely dry in the spring of 1939 (Fig. 9). Water for growth was available only in the first foot. This was soon absorbed and by the end of May available moisture occurred only in the first 6 inches. A month later there was no moisture available to a depth of four feet and less than 2 percent was present in the fifth foot. By the end of August more than 5 percent available water occurred in the upper 6 inches as a result of 3.5 inches of rain received during the month.

The precipitation, although normal in amount in 1940, was not sufficient to penetrate deeper than one

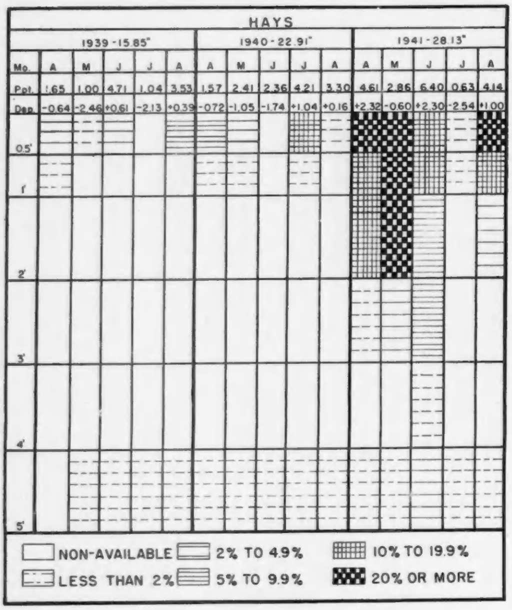

Fig. 9. Available soil moisture to a depth of 5 feet in the short-grass type at Hays.

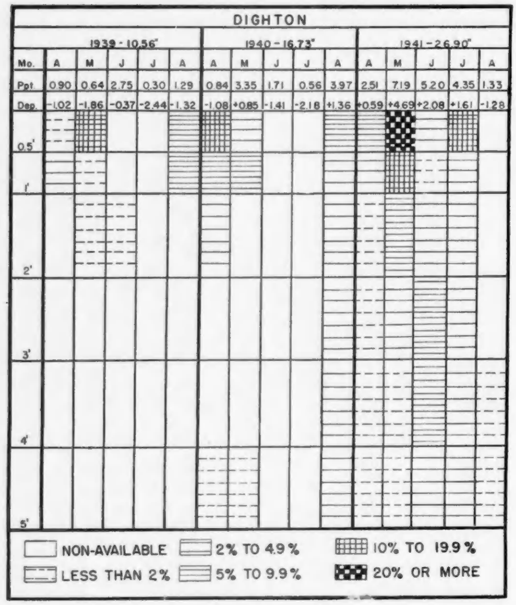

Fig. 10. Available soil moisture to a depth of 5 feet in the short-grass pasture at Dighton.

foot, and the available soil moisture was less than 10 percent in April. It was less than 5 percent in May and there was none in June. Total rainfall of 4.2 inches in July resulted in more than 10 percent available moisture in the upper 6 inches, but less than 2 percent in the second six-inch layer. This moisture was quickly absorbed or evaporated and only a small amount was found in August.

Precipitation during the winter and early spring of 1941 greatly increased the moisture content in the first two feet of soil. The supply was further augmented in May when more than 20 percent available water occurred to a depth of 2 feet, and the third foot had nearly 5 percent. Water content in June was somewhat less than in May in the upper 3 feet, but for the first time since 1933 available soil moisture was present to a depth of 5 feet. The drought of July coupled with the rapid growth of vegetation reduced the amount of available moisture nearly to zero. During August, with rainfall of more than 4 inches, the amount of available water increased to about 20 percent in the first foot and to a smaller amount in the second.

At Dighton available soil moisture extended to a depth of only a foot in April, 1939 (Fig. 10). It increased during May, but was exhausted in the upper foot during June. The continuous drought resulted in no available moisture in July. Showers during August increased the available moisture content in the surface foot to nearly 10 percent.

Available moisture was found to extend to a depth of 2 feet in April, 1940. This was slightly reduced during succeeding weeks and only a small amount was available in May in the upper 6 inches but nearly 10 percent in the second six-inch level. No available water was present when samples were taken in June and July, 1940. This extreme drought caused the prairie vegetation to become completely dormant. August had a total rainfall of nearly 4 inches and available moisture was restored to a depth of 5 feet.[2]

The available soil moisture occurring in August was maintained with only a slight decrease during the winter of 1940-1941. Hence, when samples were taken in April water was found to be available, although in small amounts, to 5 feet. The well distributed rains of May totaled over 7 inches. This not only increased the amount of available soil moisture to more than 20 percent in the upper 6 inches but also replenished it to a depth of 3 feet. During June and July moisture was slightly less than in May, but it was always available to 5 feet in depth. The only drought of the season occurred during August when water became unavailable to 3 feet, with only a small amount available at greater depths.

Temperature, Evaporation, and Wind

Mean annual temperature for 1939 ranged from 2.8° to 3.4° F. above normal at the several stations. The greatest departure from the normal occurred at all stations during May, June, July, and September. For example, the temperature was 7.7° F. above normal during May at Phillipsburg. Temperatures during the growing season of 1940 although usually above normal were lower than in 1939. During May,

[2] Cracks and fissures, often concealed at the surface, frequently occurred in the thoroughly dried soils and permittted runoff water to enter and moisten the soil deeply in some places, but not generally.

1941, the temperature ranged from 3.2° to 4.8° F. above normal at the five stations, but during June and July it was never more than slightly above and frequently below normal. During August and September the temperature was 1° to 2° above normal.

Total seasonal evaporation at Hays in inches from April to September, inclusive, was 60.7 in 1939, 49.2 in 1940, and 43.7 in 1941. Evaporation by months ranged from 5.8 to 13.6 inches the first year and was from 1 to 4 inches higher each month than during either of the two following summers. Evaporation in 1941 was lower during the early summer than in 1940 but that of August and September was somewhat higher.[3]

Wind movement at Hays from April to September, inclusive, was 39,985 miles in 1939 but only 36,621 the next year and 34,313 miles in 1941. In 1939. wind movement ranged between 6,500 and 7,100 miles each month except August when there was less. Thus, it was much windier, hotter, and drier during 1939 than during either of the two following years. In all these respects 1941 was better suited to plant growth than 1940.

TABLE 1. Percentage basal cover of each species of perennial grass in the different classes of pastures at each station, and total basal cover in 1940 and 1941.

Location and Class	Buffalo Grass		Blue Grama		Sand Dropseed		Total Cover	
	1940	1941	1940	1941	1940	1941	1940	1941
Hays 1	23.0	86.5	14.0	7.6	0.0	0.0	37.0	94.1
Hays 2	10.3	33.1	13.1	10.7	0.0	0.0	23.4	43.8
Hays 3	0.1	0.0	9.3	33.9	0.6	6.8	10.0	40.7
Hays 4	4.6	45.1	0.0	0.0	0.0	4.0	4.6	49.1
Ness City 1	4.2	28.3	14.4	15.0	0.0	0.0	18.6	43.3
Ness City 2	3.2	22.1	6.8	19.1	0.0	0.0	10.0	41.2
Ness City 3	8.3	38.3	4.3	12.1	0.0	0.0	12.6	50.4
Ness City 4	0.5	11.1	1.5	5.2	0.0	0.0	2.0	16.3
Quinter 1	1.6	14.1	2.3	4.0	1.8	17.1	5.7	35.2
Quinter 2	0.8	9.1	2.5	13.0	0.0	0.4	3.3	22.5
Quinter 3	7.9	27.1	1.9	7.4	0.0	0.0	9.8	34.5
Quinter 4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dighton 1	4.6	43.5	6.0	11.0	0.0	0.0	10.6	54.5
Dighton 2	15.4	74.7	3.8	3.1	0.0	0.0	19.2	77.8
Dighton 3	15.1	46.6	5.9	4.0	0.0	0.8	21.0	51.4
Dighton 4	0.0	0.0	2.2	3.4	0.0	0.0	2.2	3.4

BASAL COVER AND COMPOSITION OF VEGETATION

The mixed prairie of Kansas before and during the drought has been described (Weaver & Albertson 1936; Albertson 1937, 1938, 1939, 1941; and Albertson & Weaver 1942). The predrought average basal cover of the short grasses in 1932 varied between 80 and 95 percent. The extreme drought during the succeeding years greatly reduced the cover. The amount of decrease varied with the intensity of grazing and dusting. In places where judicious range management was practiced and where the pastures were naturally protected from dust blown from cultivated fields, reduction in cover was small. In other pastures, however, where the plants were weakened and coverage by dust was pronounced, the native plant population was reduced almost to zero. The cover and composition of the pastures studied at Hays, Ness City, Quinter, and Dighton follow in order. In the spring of 1940 each pasture was carefully examined before the quadrats were selected. They were samples of areas which most nearly coincided with the average conditions in the particular pasture.

HAYS PASTURES

Class 1 pasture was given the best care possible during the drought, and the cover in the summer of 1939 was much above normal for ranges in that section of the state. Extended drought in the fall of 1939, however, caused a decrease in the amount of vegetation, and in the fall of 1940 the total cover of short grass was only 37 percent (Table 1). Of this amount, buffalo grass constituted 23 percent; the remaining 14 percent consisted of blue grama. Where lack of soil moisture and not dusting was the cause of the decrease in cover, the individual bunches of grass were not killed but only reduced in size (Fig. 11A).

In pastures where drought and dusting were extreme, the cover of blue grama usually was greater than that of buffalo grass. In the better pastures, however, the reverse was frequently true. The continuous, fairly dense cover of short grass prevented any great amount of invasion of weedy annuals. In the spring of 1940, the class 1 range at Hays was sparsely populated with annuals, especially *Hordeum pusillum, Lepidium densiflorum,* and *Lappula occidentalis.* Nowhere, however, was this crop of weeds detrimental to the pasture grasses. The favorable growing conditions of 1941 were all that were needed to promote a good growth of buffalo grass. The cover of this short grass increased to 86.5 percent, while during the same period that of blue grama was reduced from 14 to 7.6 percent.

In class 2 pasture, the amount and composition of basal cover were similar before the drought to that of class 1. The reduction in 1940, or earlier, was considerably greater, however, due to adverse environmental conditions. The total cover of short grass in 1940 was only 23.4 percent and consisted mostly of small scattered tufts (Fig. 11B). In most locations the cover was rather evenly divided between the two dominants, but frequently a pure stand of one species took possession of areas varying from one to several square meters in extent. Here, as in class 1 pasture, the blue grama lost considerably during the growing season of 1941. Conversely, buffalo grass made a great increase and had an average cover of 33.1 percent when charted in the fall.

[3] Data on evaporation and wind movement were obtained from measurements made at Hays, Kansas, by Division of Dry Land Agriculture, Bureau of Plant Industry, U. S. Department of Agriculture.

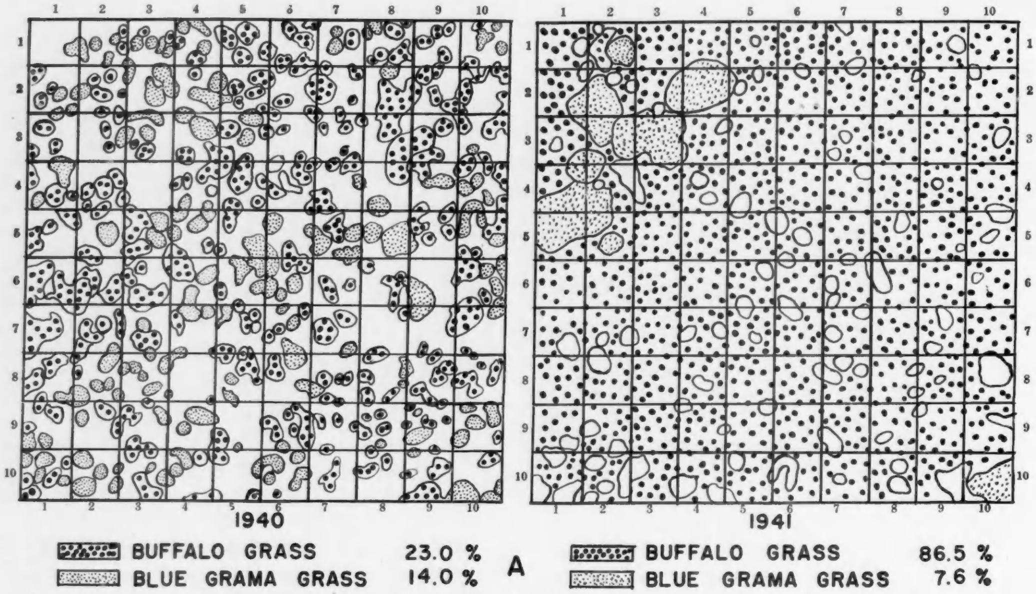

Fig. 11A. Typical meter quadrat showing basal cover of short grass in a class 1 pasture at Hays.

In class 3 pasture buffalo grass had nearly disappeared. Blue grama constituted only 9.3 percent and sand dropseed .6 percent. The basal cover and the composition varied so greatly in these dusted areas that it was difficult to select any quadrat that was representative of the area as a whole. The presence of sand dropseed was common to all quadrats, but in some either remnants of buffalo grass or small tufts of blue grama were present. The condition where blue grama formed a greater cover than that of buffalo grass is typical for this area (Fig. 11C). The growth of blue grama during 1941 was phenomenal; its cover increased to 33.9 percent by fall. The number of tillers in each tuft increased manyfold and, as a consequence, the peripheral area occupied by each bunch was extended greatly. It seems that blue grama retained good vitality where it was not buried too deeply by dust, and when the rains came

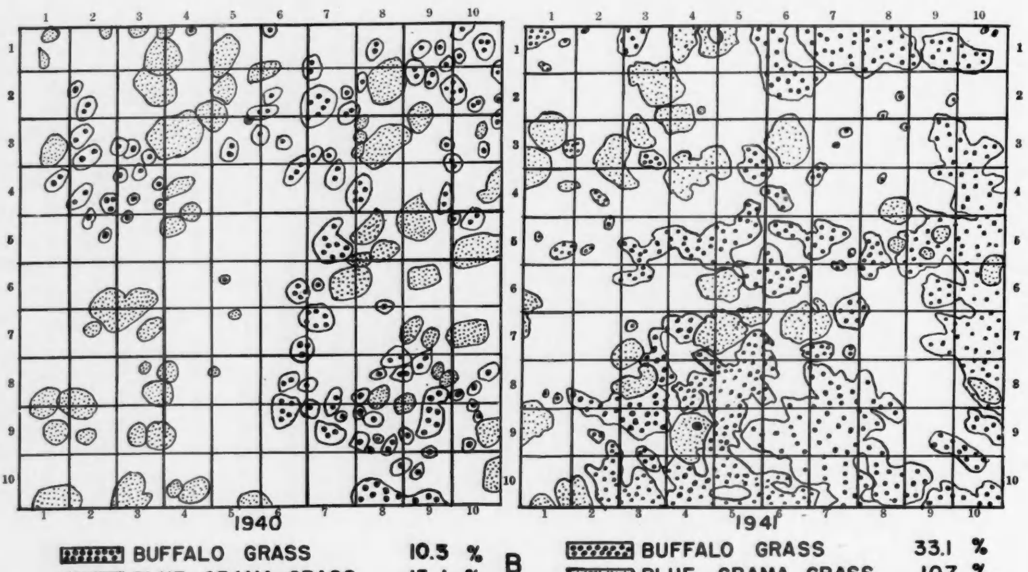

Fig. 11B. Meter quadrat showing open cover of short grass in a class 2 pasture at Hays.

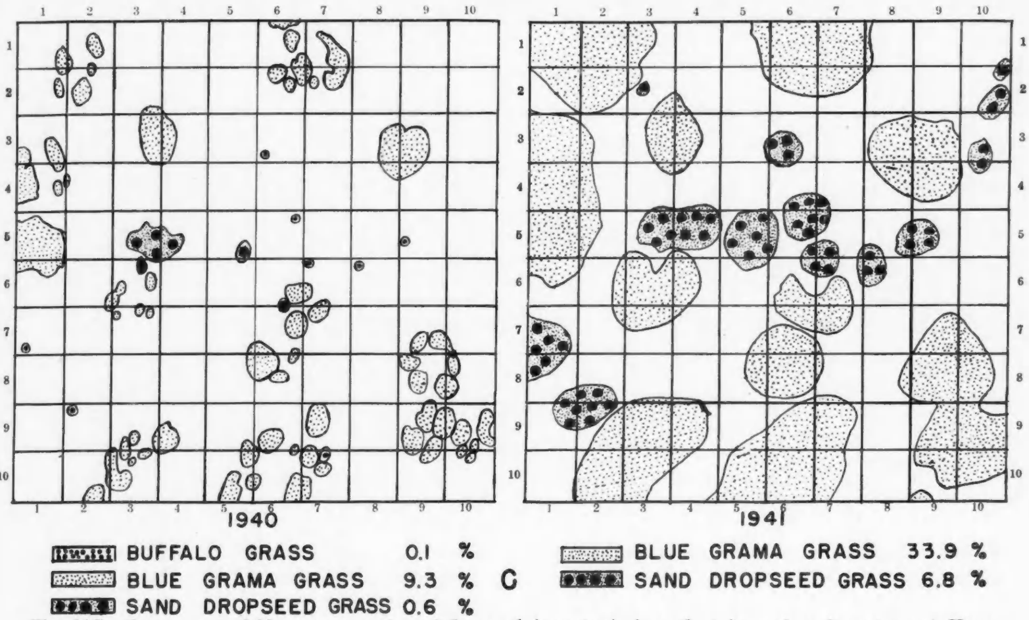

Fig. 11C. Open cover of blue grama and sand dropseed in a typical quadrat in a class 3 pasture at Hays.

to this rich soil it grew vigorously. This is quite in contrast to its losses in the other quadrats. Sand dropseed had also made fairly large gains and constituted 6.8 percent cover.

Class 4 pasture was located on rather low ground where both mid and tall grasses were formerly common. Due to intensive grazing, however, the composition of this area had gradually changed from that of mid and tall grasses to one of short grasses. The cover had been dense, perhaps 80 to 90 percent, until several years after the beginning of the drought in 1933. The storms of 1935 deposited a thick layer of fine dust over most of this entire area. In many places the native vegetation was completely smothered, in others only small remnants remained. The condition that prevailed in the fall of 1940, when the first charting was done, represented the cover not at its worst but after considerable improvement had taken place during the normal growing season of 1940. The cover of buffalo grass, however, was only 4.6 percent and no blue grama occurred. Seedlings of sand dropseed were present (Fig. 11D). The small scattered bunches of buffalo grass grew vigorously through the favorable season of 1941 and covered nearly half the soil when charted in the fall. Sand dropseed increased from a few seedlings to a cover of 4 percent.

The absence of blue grama and the presence of so small an amount of buffalo grass in 1940 resulted from heavy dusting and much overgrazing. Dusting in 1935 was so great that every vestige of native prairie vegetation was removed. Buffalo grass invaded these barren areas much more rapidly than did blue grama during the less severe drought years, such as 1938, and had made some growth during 1940 before it was charted in the fall. The rapid increase of basal cover from 4.6 percent the first year to 45.1 in 1941 is eloquent testimony of the recuperative powers of buffalo grass.

NESS CITY PASTURES

Intensity of grazing of the pastures near Ness City was similar to that at Hays. The degree of dusting, however, was considerably more intense. Pastures not severely dusted during the period of drought, and particularly in 1935, were found only with great difficulty; in fact, the condition that prevailed was one where there was not only a rather continuous layer of dust to a depth of 1 to 3 inches but also great drifts extending in various directions across the range. The characteristic damage from such layers and drifts was the complete obliteration of all vegetation over comparatively large areas. It was not uncommon to find nearly level tracts, even 160 acres in extent, where no native vegetation remained except on sharp inclines where dust failed to accumulate.

Class 1 pasture at Ness City had been given the best treatment that could be found in the locality. Light grazing was common and deferred grazing had been practiced occasionally. Studies had been made in this pasture several years previous to 1939. The average cover in 1937 was about 5 percent. It consisted mostly of blue grama and buffalo grass. The favorable growing conditions during 1940 resulted in a considerable increase, and when charted in the fall a total basal area of 18.6 percent was found. It was composed of 4.2 percent buffalo grass and 14.4 blue

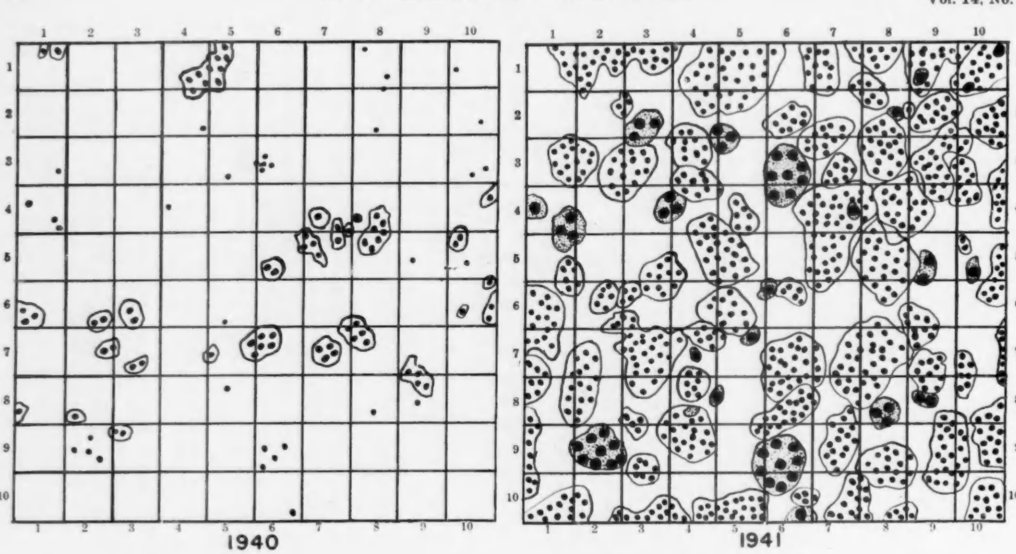

Fig. 11D. Quadrat at Hays where the short grass cover had been greatly reduced.

grama (Fig. 12A). In 1941 the amount of vegetation had increased to 43.3 percent, 28.3 being buffalo grass and 15.0 blue grama. The increases occurred mainly through the enlargement of small tufts of grass that were alive in the fall of 1940. In many places, the spread of buffalo grass was very vigorous and greatly exceeded that of blue grama. In fact, when charted in the fall of 1941, some of the bunches of blue grama had disappeared.

In 1940, the cover in class 2 pasture was only 10 percent, about one third was buffalo grass and two thirds blue grama (Fig. 12B). The characteristic small, isolated tufts of grass prevailed. The increase during 1941 was not equally shared by both short grasses, since buffalo grass increased sevenfold. Of the total cover of 41.2 percent, buffalo grass constituted 22.1 and blue grama 19.1 percent. Tufts of short grasses were less numerous in 1941 than in the

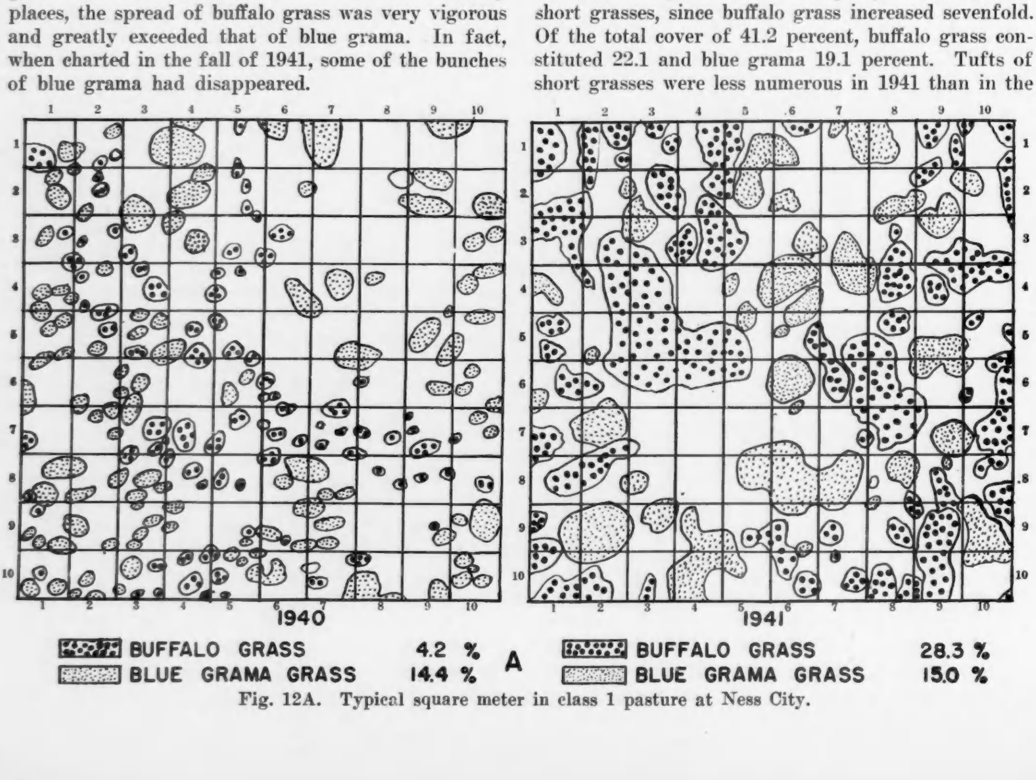

Fig. 12A. Typical square meter in class 1 pasture at Ness City.

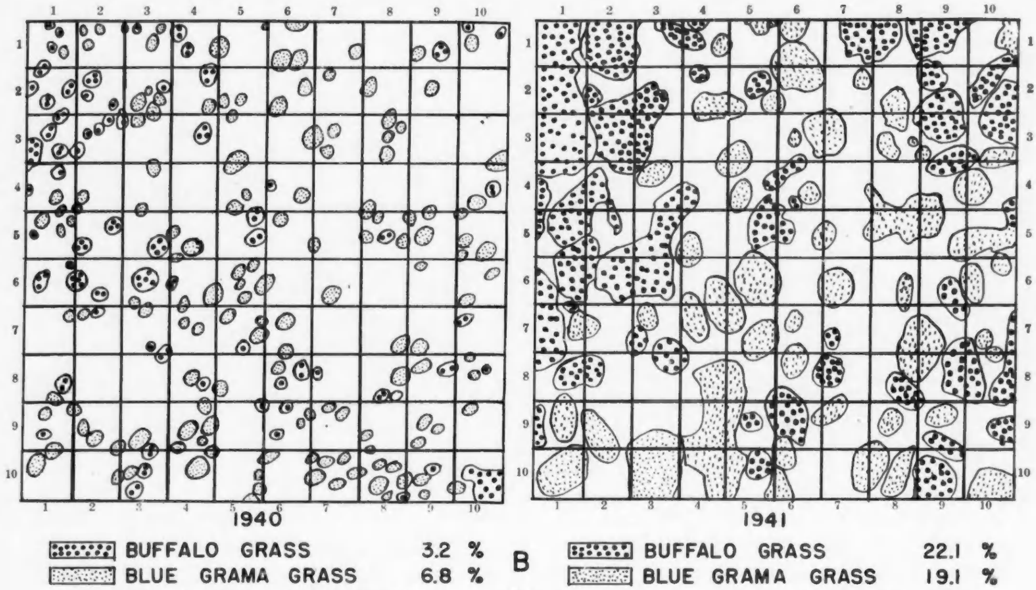

Fig. 12B. Quadrat typical of class 2 pasture which w as less than a mile from the class 1 pasture.

previous year. This doubtless resulted from the merging of the smaller ones through growth.

Cover in class 3 pasture had been materially reduced during the dry years and especially in 1939. In the fall of 1940 it was 12.6 percent; 8.3 percent was buffalo grass and only 4.3 blue grama (Fig. 12C). In 1941 the cover of buffalo grass had increased to 38.3 percent but that of blue grama only to 12.1, making a total basal cover of 50.4 percent.

Native vegetation in class 4 pasture had been completely destroyed over large areas and it was with considerable difficulty that representative quadrats were located. The one shown in Figure 12D represents conditions better than the average. Basal area in 1940 was only 2 percent, being composed of 1.5 percent blue grama and .5 of buffalo grass. Of the total of 16.3 percent cover in 1941, blue grama constituted 5.2 and buffalo grass 11.1 percent. Thus,

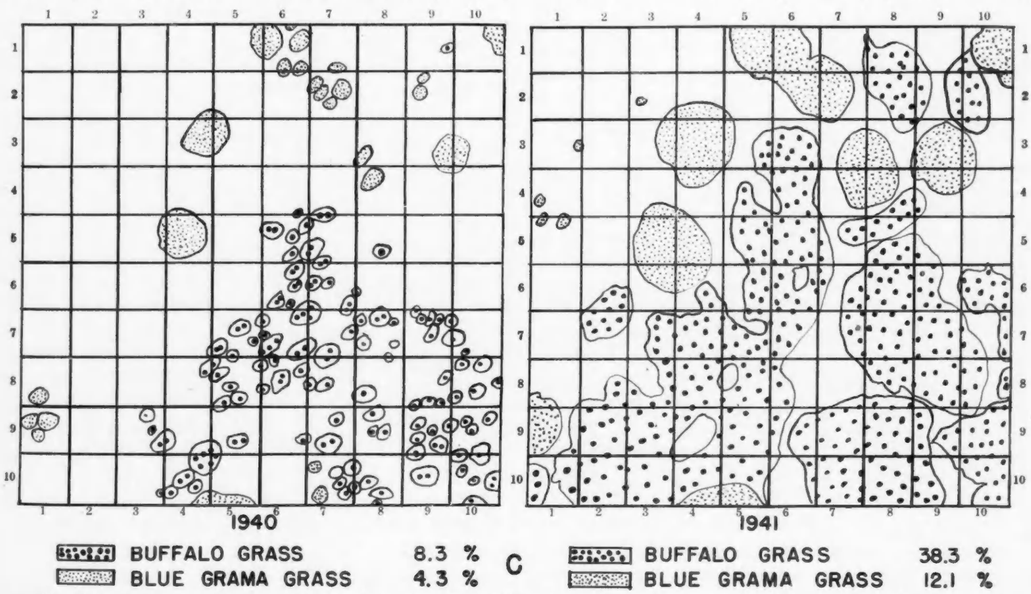

Fig. 12C. Square meter area in class 3 pasture near Ness City where heavy grazing had greatly reduced the cover in early years of the drought.

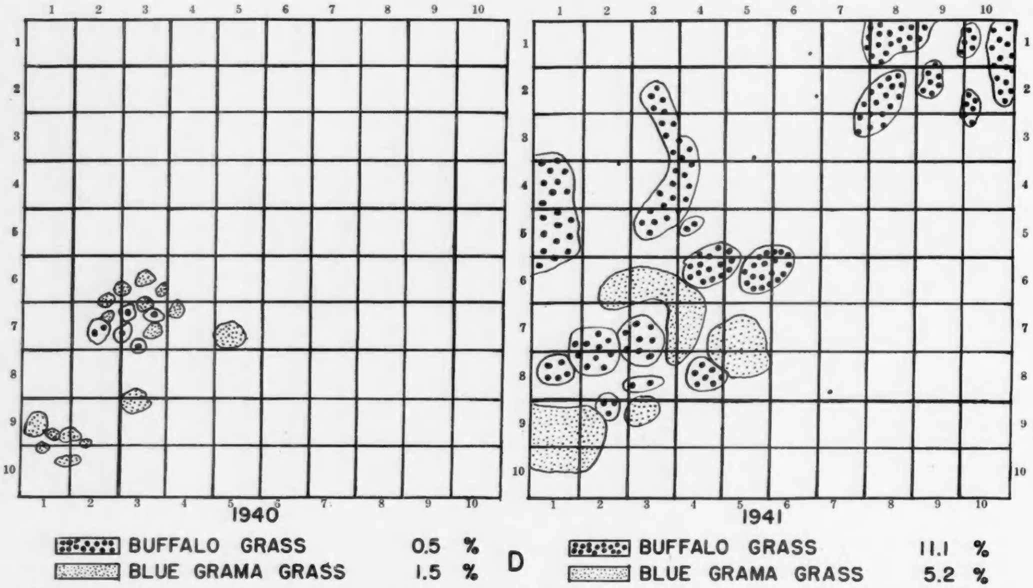

Fig. 12D. Typical quadrat in class 4 pasture at Ness City. There was no native vegetation in most of the area.

in all four pastures both species of short grass made good gains, but those of buffalo grass were the greater.

Quinter Pastures

Pastures in the vicinity of Quinter showed considerable variation in the intensity of grazing and amount of dusting. Those on rolling topography, which were usually largest, suffered least from adverse environmental conditions. Even under the most favorable circumstances, however, the extreme drought of 1939 destroyed much of the grass. In the spring of 1940, a large percentage of the short grass on the better pastures had lost the golden straw color which characterizes it when it is dormant but alive. Improvement during 1940 was extremely slow, due to the greatly weakened condition of the vegetation. It seemed as if the urge to grow had been almost completely lost by the drought-resistant relicts even though the plants were still alive.

Pastures on level or only slightly rolling topography were usually subjected to the most intense grazing and dusting, and consequently had suffered the greatest amount of damage. Frequently where the original vegetation had been largely or totally destroyed some of it was replaced by invading perennials such as *Sporobolus cryptandrus, Schedonnardus paniculatus,* or in extreme cases, by weedy annuals—often *Salsola pestifer, Helianthus annuus, Chenopodium album,* and *Amaranthus retroflexus.*

Class 1 pasture had an average cover of 5.7 percent in 1940. Buffalo grass was present throughout, but it was often concentrated in groups of small tufts. In Figure 13A, its average cover was only 1.6 percent. Blue grama furnished a cover of 2.3 and sand dropseed 1.8 percent. In the fall of 1941 buffalo grass had increased to 14.1 percent and blue grama to 4. Sand dropseed had made a rather phenomenal growth, and even exceeded buffalo grass in increasing its area.

Although class 2 pasture had not been seriously overgrazed according to stocking records, continuous drought, especially in the fall of 1939, had nearly destroyed all vegetation. Relict plants were so weakened that the rainfall of 1940, even though nearly normal, failed to produce any improvement. When charted in the fall, the total cover was only 3.3 percent (Fig. 13B). The gain during 1941 was somewhat below normal, due no doubt to the weakened condition of the grasses. The cover of buffalo grass was only 9.1 percent in 1941 and that of blue grama 13. Sand dropseed had only .4 percent basal cover.

Class 3 pasture, where dusting was much more severe than in either of the preceding, apparently did not suffer so greatly from the 1939 drought. Amount of vegetation in 1939 was considerably less than in the other pastures but the improvement during 1940 was much greater. Consequently in the fall of 1940, buffalo grass (7.9 percent) was much more abundant than in the better classes of pastures. During the next season it increased to 27.1 percent and blue grama to 7.4 (Fig. 13C).

Class 4 pasture had no native grass in its cover during either of the two years. Improvement in other pastures at this station occurred almost entirely in 1941, so severe had been the drought. But in 1941 good growth occurred, the gains made by buffalo grass equalling or exceeding those of blue grama.

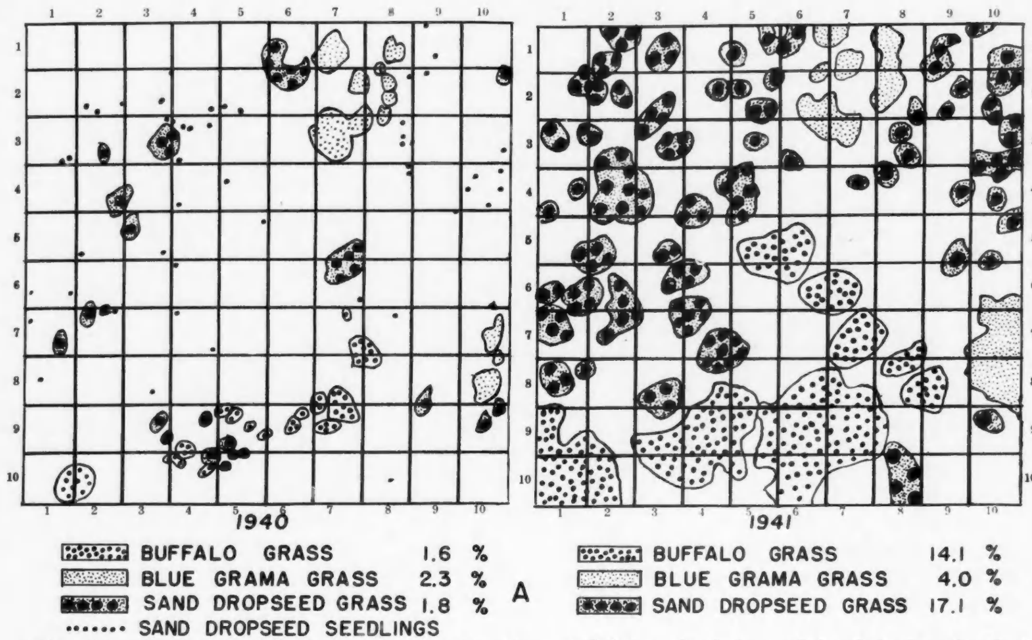

Fig. 13A. Quadrat typical of cover in class 1 pasture at Quinter. Sand dropseed invaded when the short grasses were killed.

DIGHTON PASTURES

Range lands near Dighton had suffered somewhat less from dusting than those at Ness City, 30 miles eastward. Exceptions were pastures surrounded by cultivated fields. These had experienced extreme losses.

Class 1 pasture had not only been stocked lightly through most of drought years but it was surrounded

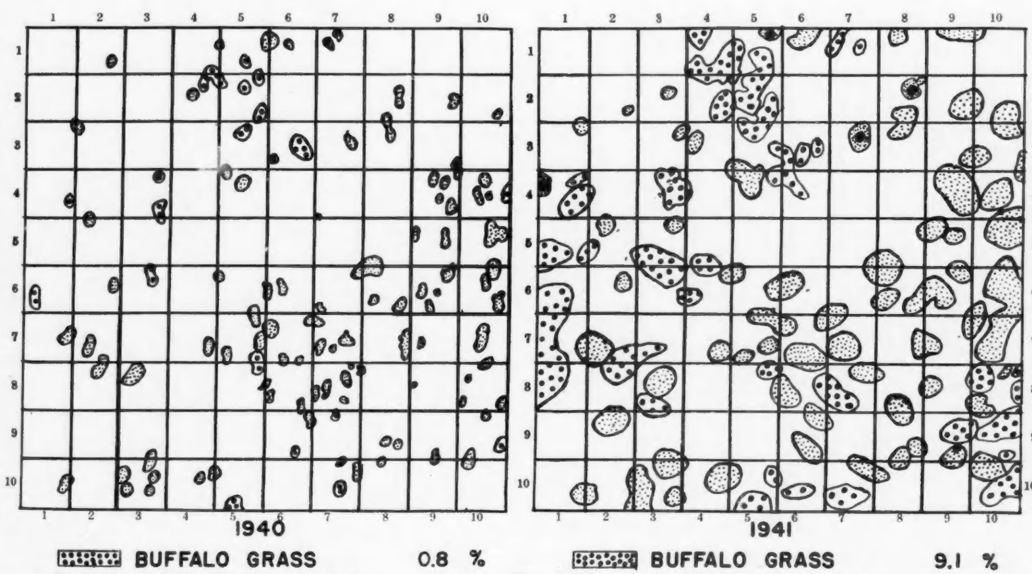

Fig. 13B. The small tufts of short grass in this class 2 pasture quadrat at Quinter are typical of ranges where drought had been severe. Where the damage was caused by dust the tufts were usually farther apart.

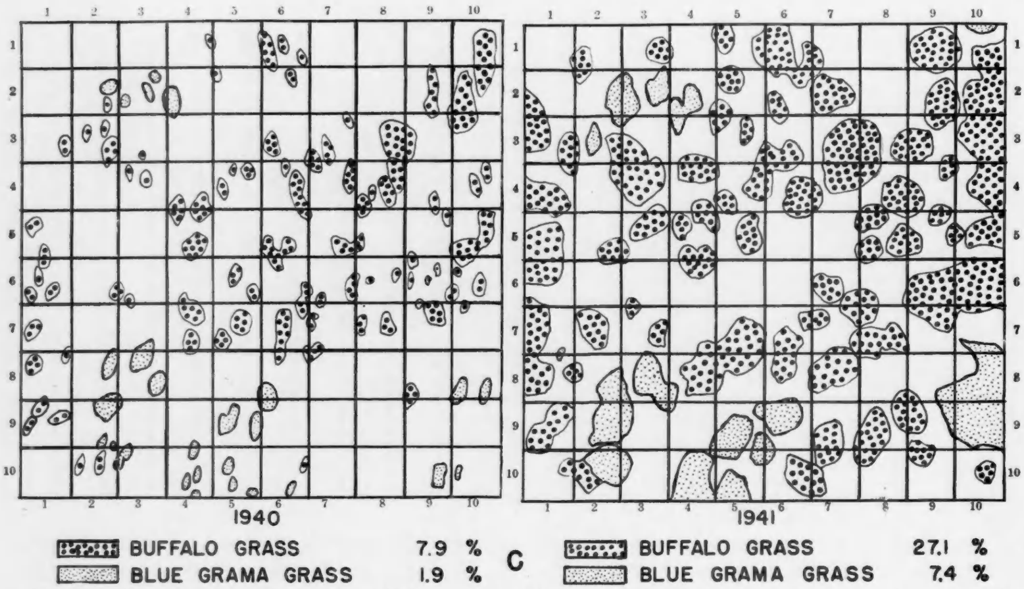

Fig. 13C. Class 3 pasture at Quinter which was dusted badly in 1935. The cover was uneven because of the destruction of vegetation by dust.

by other pastures. Therefore the intensity of dusting was reduced to a minimum in comparison with that of the other prairie land in the community. The cover of the pasture was from 15 to 20 percent in 1939 (Fig. 14A). The loss during the late fall, however, was severe and growth during 1940 was meager in comparison with that of nearby pastures. This was due primarily to variations in local showers. The cover in the fall of 1940 was only 10.6 percent, 6 percent of which was blue grama and 4.6 percent buffalo grass. The excellent environmental conditions during the summer of 1941 resulted in vigorous growth. The small tufts of blue grama were greatly enlarged and the cover in 1941 was increased to 11 percent. Buffalo grass increased in the usual manner, sending out myriads of long stolons. Its basal area increased to 43.5 percent.

Changes of cover in this pasture were given further study. The remarkable increase in basal area from less than 1 percent in August, 1940 (which was only about one tenth of that in late fall recorded above), to 80 percent in July, 1942, has been recorded by photographs. The severe drought in the fall of 1939 reduced the cover of about 18 percent to only 1 percent by August of the next year (Figs. 14A and B). This left nearly all of the soil exposed to erosion. The rains during the spring of 1940 were sufficient to cause the soil to form a crust and thus become especially susceptible to loss of moisture through evaporation. The dark areas in Figure 14B are due to flaking of the surface soil and its removal by wind. This process has furnished abundant materials for many dust storms. The increase in cover during 1940 occurred because of ample rains in August and September. The basal area of vegetation increased to about 11 percent (Fig. 14C). The increase was due not only to the enlargement of each tuft of grass but also to an actual increase in the number of tufts through revival of the half dead crowns just beneath the surface of the soil. Growth began early in 1941. By the last of May the ground cover had increased to about 20 percent. Rapid growth occurred during spring and early summer and in early July the cover averaged 30 percent. Another 10 percent was added before the short period of drought occurred in August. Further plant growth in the autumn occupied another 15 percent of the bare soil. Tufts of buffalo grass had rapidly developing stolons projecting outward in every direction. These leafy offshoots formed approximately four fifths of the total basal area. Still further improvement in the vegetation in July, 1942, is shown in Figure 14D when perennial pasture grasses, mostly buffalo grass, covered 80 percent of the soil.

Although the original basal area was nearly restored by midsummer of 1942, its composition was very different from that at the beginning of the drought. In 1933, buffalo grass and blue grama were about equally represented. In 1942 the former comprised at least 75 percent of the mixture of the two dominants. Perennial forbs had been almost exterminated.

In class 2 pasture, ground cover was 19.2 percent in the fall of 1940. Blue grama constituted 3.8 percent and buffalo grass 15.4. The greater amount of buffalo grass was doubtless due to the increase of this species during the summer. Blue grama was

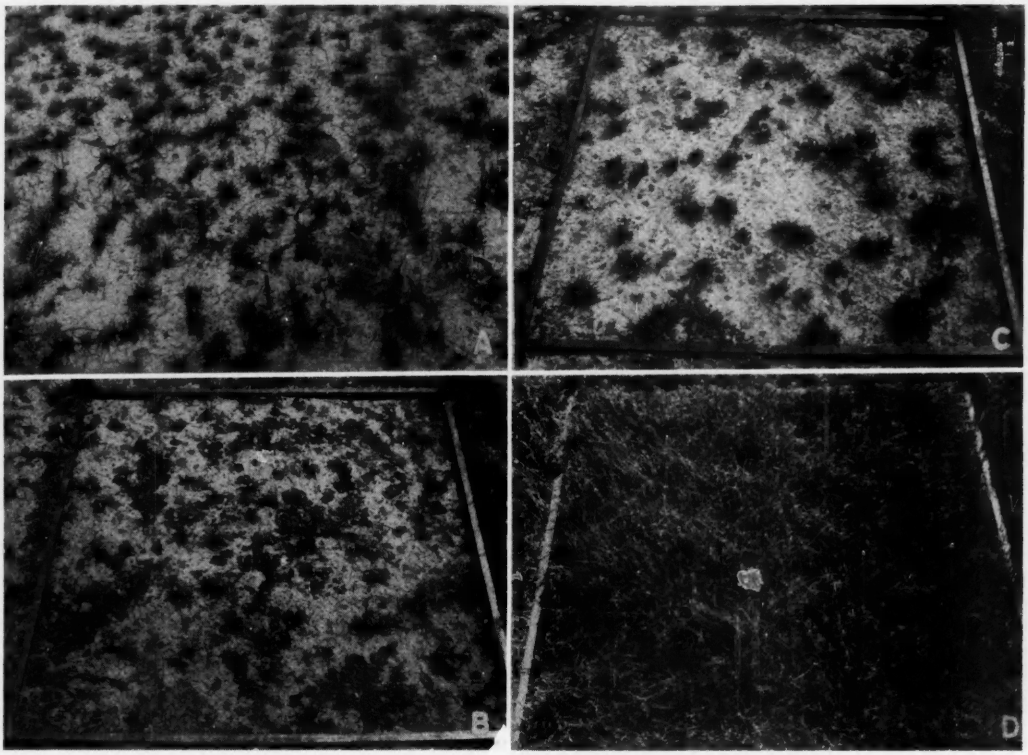

FIG. 14. A. View of short grass in class 1 pasture at Dighton in September, 1939, when the basal cover was 15 to 20 percent. B. Quadrat in class 1 pasture at Dighton on August 1, 1940, before any recovery had occurred from the drought of 1939. Basal cover is 1 percent. Note the loss of surface soil. C. Same quadrat as in B. The cover is now 10.6 percent, an increase of tenfold in 60 days. Photo September 28, 1940. D. Same quadrat as it appeared on July 7, 1942. Buffalo grass has increased greatly and the basal cover is 80 percent.

reduced to 3.1 percent in 1941, but buffalo grass increased nearly fivefold and composed 74.7 percent of the grass when charted in late fall.

In class 3 pasture, the cover was 21 percent in 1940. Here again, buffalo grass furnished the larger amount. It grew rapidly during the season of 1941 and increased its initial cover of 15.1 percent to 46.6. The number of tufts of blue grama was reduced considerably, but due to the enlargement of those that did survive the former cover of 5.9 percent was decreased only about one third.

Class 4 pasture had been closely grazed for many years. Dusting, particularly in 1935, was very severe. The drifts of soil were so high and numerous that it was impossible to drive over this area for several years following the worst storms. The native plants were completely smothered over most of the pasture. The cover, largely blue grama, was never greater than 3.4 percent (Table 1).

This group of pastures represents well the drastic changes that the vegetation had undergone, the actual loss or at least slow recuperation of blue grama which was all but destroyed, and the extremely rapid recovery and wide spread of buffalo grass as soon as conditions favorable to its growth occurred.

DISCUSSION

The pastures were examined in the fall of 1939 when the drought was so intense that it was impossible to separate with certainty living, dormant plants from those that were dead. Although the plots were selected and fenced in early spring of 1940, amount of living vegetation could not be determined until the occurrence of rains and revival of the vegetation. It was for this reason that quadratting was not done until fall. Hence, the basal area was measured only after a summer of very variable growth under subnormal and unevenly distributed rainfall. Consequently, although the cover was invariably least in class 4 pastures it was not always greatest in class 1. The exceptions were at Quinter where the class 3 pasture recovered best, and at Dighton where both class 2 and 3 pastures had nearly twice as much cover as class 1. If the 16 pastures at all four stations are considered together as a sampling of a very large range area, then the average cover in 1940 in classes 1 to 4 was 18.0, 13.7, 13.4 and 2.2 percent, respectively.

When in 1941 an excellent season for growth occurred after nine or more dry years, these pastures

extended their cover to 56.8, 46.3, 44.3, and 17.2 percent, respectively. The grasses in class 1, 2, and 3 pastures tripled their basal cover, those in class 4 increased nearly eightfold. Increases in most of the individual pastures were twofold (only one less) to fourfold. Class 1 pastures at Quinter and Dighton increased their previous cover approximately 6 and 5 times, respectively, and class 4 at Ness City 8 times. Class 2 at Quinter, where growth the previous year in all pastures was poor, increased its cover sevenfold, and the cover in class 4 pasture at Hays became ten times as great in a single summer.

These results illustrate the wonderful recuperative powers of both blue grama, the most drought resistant species of the midwest (Mueller & Weaver 1942), and buffalo grass, which spreads vegetatively with great rapidity. Except for sand dropseed, which occurred in certain pastures and has during the past few years spread widely over the plains, it seems certain that seedling grasses played a very minor role in the process of recovery. This is in agreement with the earlier extensive work of Savage (1937) and Weaver and Albertson (1936). Albertson and Weaver (1942) in their seven-year study of ranges in Kansas, state: "Despite quantities of seedlings, and rapid propagation of buffalo grass by stolons in 1935 and at other times, periods favorable to growth were usually too short to result in establishment. Flower stalks were sometimes formed but few seeds matured. With dusting and denudation rainfall became less efficient and runoff greatly increased." Weaver and Mueller (1942) ascertained that the average distribution of perennial grass seedlings in mixed prairie in June, 1941, was only 2.4 per square foot. They state that the probability of the seedlings of the dominant range grasses completing their life cycle by production of seeds the first year is remote, since a continuous moisture supply rarely occurs. Even if all the seedlings of perennial grasses (exclusive of the stoloniferous buffalo grass) had survived and made a maximum growth they would have increased the cover less than two percent.

Since most of the increase in cover was due to buffalo grass, its abundance in the several pastures as compared with blue grama is important. In the fall of the first year, blue grama exceeded buffalo grass in abundance in all class 1 and 2 pastures, except class 1 at Hays and class 2 at Dighton. Average amount of each short grass in the group of four class 1 and four class 2 pastures was about the same. At the end of 1941 there was about 4.5 times as much buffalo grass as blue grama in the average of class 1 pastures and about 3 times as much in the average of class 2 pastures. Moreover, the buffalo grass exceeded blue grama in amount in 7 of the 8 pastures of the first and second classes. In the average of class 3 and 4 pastures in 1940, buffalo grass ranked greater in basal cover than blue grama in the ratio of about 3 to 2 and 5 to 4, respectively. Blue grama ranked first in only 2 individual ranges. Buffalo grass was not represented in one class 3 pasture either in 1940 or 1941. Otherwise it was most abundant in all in 1941, and its average basal cover was nearly 5 times that of blue grama in the other three pastures. The grasses in only a single pasture in class 4 may be compared in 1940 since either one or the other of the short grasses was absent in three. But buffalo grass was twice as abundant as blue grama in the fourth. Thus, buffalo grass ranked higher when it was present in 1941, in every range except one. Its average basal cover (34.3 percent) was 3.2 times greater than that of blue grama.

ANNUAL YIELD OF NATIVE GRASSES AND WEEDS

Total yields of short grass, mid grass, and weeds were obtained in each class of pasture at the several stations including Phillipsburg. All yields are expressed in pounds per acre.[4]

Hays Pastures

Class 1 range had a fairly even cover of 37.1 percent in the fall of 1940 which yielded 1,378 pounds per acre (Table 2). By 1941 the cover had increased to 96 percent but the average yield increased much less. It was 1,524 pounds (Fig. 15). It is significant that the yield of weeds (mostly *Hordeum pusillum* and *Festuca octoflora*) was only 391 pounds in 1940 but 707 in 1941. The open places in the sod were usually more densely populated by ruderals than were the smaller and less numerous ones where the cover had suffered little or no deterioration. In most locations where the cover of short grass remained nearly normal, the seeds of many weedy plants failed to make sufficient contact with the soil to insure germination. The few scattered seedlings

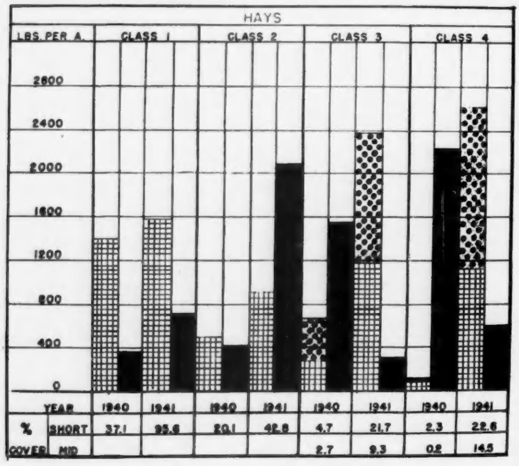

Fig. 15. Percentage basal cover and yield in pounds per acre of short grass (crosshatch), mid grass (dots), and weeds (black) in the several pastures at Hays in 1940 and 1941.

[4] Annual yields are based on a slightly different percent of cover than that given in Table 1, since more quadrats were included.

growing in these places barely survived the competition for water and light and their presence had little effect upon the growth of the native vegetation.

TABLE 2. Basal cover and plant yield in the several pastures.

Class	Year	Percent Cover		Yield In Pounds Per Acre			
		Short grass	Mid grass	Short grass	Mid grass	Total grass	Weeds
			HAYS				
1	1940	37.1	....	1,378	.....	1,378	391
	1941	95.6	....	1,524	.....	1,524	707
2	1940	20.1	....	534	.....	534	432
	1941	42.8	....	902	.....	902	2,085
3	1940	4.7	2.7	231	378	609	1,546
	1941	21.7	9.3	1,170	1,226	2,396	292
4	1940	2.3	0.2	110	23	133	2,277
	1941	22.6	14.5	1,092	1,455	2,547	596
			NESS CITY				
1	1940	21.0	....	708	.....	708	1,270
	1941	45.0	....	1,390	.....	1,390	1,729
2	1940	11.0	....	478	.....	478	1,655
	1941	42.6	....	1,610	.....	1,610	1,240
3	1940	10.2	....	459	.....	459	1,045
	1941	49.6	....	2,810	.....	2,810	650
4	1940	4.3	....	118	.....	118	892
	1941	22.0	....	752	.....	752	1,215
			QUINTER				
1	1940	4.0	3.0	99	52	151	1,890
	1941	23.7	10.0	1,081	1,517	2,598	2,099
2	1940	1.7	....	41	.....	41	1,262
	1941	18.5	....	686	.....	686	1,850
3	1940	6.9	0.2	104	.....	104	2,094
	1941	32.0	1.2	1,511	226	1,737	2,184
4	1940	....	....	.....	.....	.....	2,700
	1941	....	....	.....	.....	.....	2,010
			DIGHTON				
1	1940	10.9	....	106	.....	106	1,413
	1941	55.3	....	1,854	.....	1,854	108
2	1940	20.0	....	187	.....	187	1,233
	1941	72.9	....	2,412	.....	2,412	52
3	1940	17.0	....	184	.....	184	185
	1941	67.5	....	2,401	.....	2,401	40
4	1940	2.2	....	98	.....	98	1,210
	1941	3.4	....	360	.....	360	1,985
			PHILLIPSBURG				
1	1940	4.8	0.3	163	14	177	864
	1941	16.1	1.2	709	92	801	3,376

Class 2 pasture with an average cover of 20.1 percent yielded 534 pounds in 1940 and 902 in 1941. Here the yield increased more in proportion to increase in cover. The vegetation on this range was somewhat patchy, caused by differences in density and height of the dominants (Fig. 16). Yield of weeds in 1940 was only 432 pounds but, due to a dense stand of *Hordeum pusillum,* in 1941 it increased to 2,085 pounds.

Hordeum pusillum was often represented by 6,000 to 8,000 plants per square meter (Fig. 17). They formed a dense stand, frequently 20 inches high and resembled a field of cultivated barley. The shoots of the short grasses were dwarfed and scarcely able to carry on photosynthesis with the small amount of sunlight that diffused through the overtopping little

FIG. 16. View of class 2 pasture at Hays. Differences in height are due to alternating patches of blue grama and buffalo grass and to intensity of grazing. September, 1939.

barley. Yield of perennial grasses was materially reduced where the stand of this weed was so dense that growth in the spring was seriously delayed. The harmful effect of little barley upon the growth of the short grasses was further complicated by the fact that after ripening, early in June, it lodged and formed a dense mat which completely overtopped the short grasses.

FIG. 17. View of class 1 pasture where the short grasses are overtopped by a dense stand of *Hordeum pusillum.* More than a ton per acre of this weedy grass was often produced in pastures of west-central Kansas.

In class 3 pasture, the basal cover was considerably less than in classes 1 and 2. It had the characteristic open-bunch appearance that so often occurred when dusting had been severe. The isolated bunches of blue grama that survived the adverse environmental conditions during the previous years of drought spread rapidly, due to the growth of new tillers. Sand dropseed behaved in a manner very similar to that of blue grama. The growth of both grasses was unusually rank in 1941 which accounts for the heavy production. Yield of short grass in 1940 was only 231 pounds, but that of mid grass was 378. In 1941, yield of short grass was 1,170 pounds and that of mid grass, 1,226. Thus, the increases were about fivefold and fourfold, respectively. Yield of weeds, mostly *Lepidium densiflorum,* averaged 1,546 pounds in 1940 and greatly reduced the amount

of water available to the grasses. The unusually cool, wet spring of 1941 was not conducive to growth of weeds and their yield was reduced to only 292 pounds.

Class 4 pasture had almost no cover in the spring of 1940. Yields of short grass and mid grass during this year were only 110 and 23 pounds, respectively. In 1941 the cover of both was greatly increased. The harvest of short grass yielded 1,092 pounds and that of mid grass 1,455. Thus, the mid grass with only slightly more than half as great a basal area as short grass yielded more (Fig. 15). Sand dropseed is not only a very drought resistant species but it also furnishes a moderately good grade of forage.

Ness City Pastures

Class 1 pasture had a basal cover of 21 percent in 1940, which was the result of good management during the previous years of severe drought. The yield of short grass was 708 pounds. By 1941 the cover had increased to 45 percent and the yield to 1,390 pounds (Fig. 18). There were no mid grasses in any of the Ness City pastures. *Hordeum pusillum* formed a dense stand throughout most of class 1 pasture and yielded 1,270 pounds in 1940 and 1,729 in 1941. Thus, the yield of this weedy annual even in the best pasture type exceeded one half ton and was far greater than that of native perennials during both years.

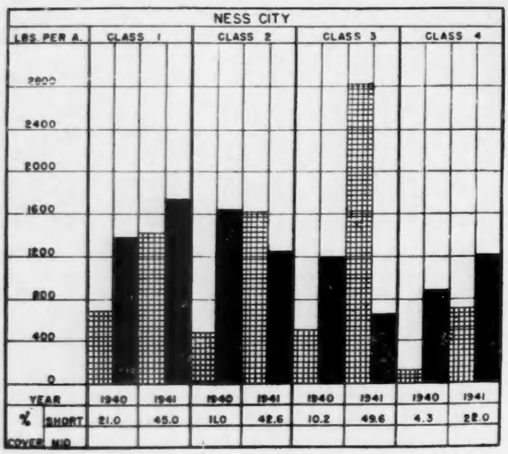

Fig. 18. Percentage basal cover and yield in pounds per acre of short grass (crosshatch) and weeds (black) at Ness City.

Class 2 pasture, located less than a mile from the first, had been subjected not only to more severe grazing but also to a greater degree of dusting. The short-grass cover of 11 percent in 1940 yielded only 478 pounds. The improvement was rapid, however, during the growing season of 1941 and the yield of short grass was 1,610 pounds from a cover of 42.6 percent. Thus, cover and yield increased in almost the same proportion. The yield of weeds, mostly *Chenopodium album*, was 1,655 pounds in 1940 but much less, 1,240 pounds, in 1941.

Cover in class 3 pasture was reduced to only 10.2 percent in 1940; the yield of short grass was 459 pounds. But in 1941 great improvement occurred, and the short-grass cover of 49.6 percent produced the very high yield of 2,810 pounds. Yield of weeds was 1,045 pounds in 1940 but only 650 in 1941.

Class 4 pasture had a sparse initial cover of 4.3 percent. Growth was slow and an average acre yield of only 118 pounds was harvested during 1940. The cover had increased to 22 percent in 1941 from which 752 pounds of short grass were harvested. The weed population was composed of *Chenopodium album*, *Helianthus annuus*, *Salsola pestifer*, *Eragrostis cilianensis*, and *Euphorbia marginata* (Fig. 19). A total of 892 and 1,215 pounds was harvested during the seasons of 1940 and 1941, respectively.

Fig. 19. Class 4 pasture at Ness City in August, 1941. Much of the soil had been partially reclothed with buffalo grass.

The variability of the weed population in these disclimax short-grass prairies, where half or less than half of the surface was occupied, is shown by the great variation in the production of ruderals. Under conditions 1 and 4 (Table 2) the population of weeds increased in 1942 over that of the previous year, while under conditions 2 and 3 it diminished.

Quinter Pastures

Class 1 pasture had been subjected to severe dusting in 1935, but to little thereafter. Grazing was moderate. The 4 percent basal cover of short grass yielded only 99 pounds in 1940 and a 3 percent cover of mid grass *(Sporobolus cryptandrus)* 52 pounds (Fig. 20). Both species made considerable gains in 1941 when the cover was 23.7 and 10 percent, respectively. The yield of short grass was 1,081 pounds and that of the mid grass, 1,517. *Lepidium densiflorum*, *Monolepis nuttalliana*, and other weeds yielded 1,890 pounds in 1940 and 2,099 in 1941.

A cover of 1.7 percent in class 2 pasture yielded only 41 pounds in 1940. The basal area increased to 18.5 percent in 1941 and the yield to 686 pounds. Thus, the basal area was 11 times greater and the

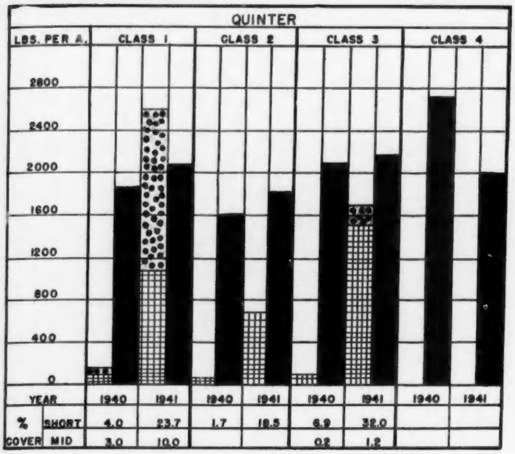

FIG. 20. Basal cover and yield in pounds per acre of short grass (crosshatch), mid grass (dots), and weeds (black) at Quinter.

yield about 17 times more than in the preceding year. There was a heavy yield of weeds each year, 1,262 and 1,850 pounds, respectively.

Class 3 pasture had been grazed similarly to that of class 2 but the degree of dusting was much greater, in fact, large drifts of soil were common. The damage from the drought of 1939 appeared to be less on this area than on class 2 pasture. The cover of short grass in 1940 was 6.9 percent, and it yielded 104 pounds. Basal cover increased to 32 percent in 1941 and the acre yield to 1,511 pounds. The cover of *Sporobolus cryptandrus* was negligible in 1940 but by 1941 it was 1.2 percent and yielded 226 pounds. Weeds in 1940 were composed primarily of *Salsola pestifer, Amaranthus retroflexus,* and *Chenopodium album* (Fig. 21). Yields in 1940 and 1941 were 2,094 and 2,184 pounds per acre, respectively. Thus, the foliage cover in all the Quinter pastures was high and to the casual observer their condition appeared to be good.

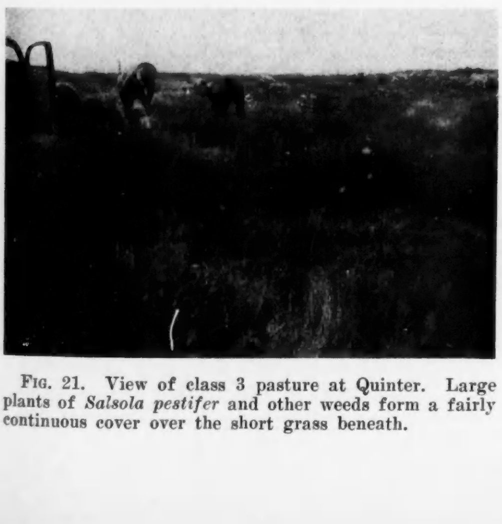

FIG. 21. View of class 3 pasture at Quinter. Large plants of *Salsola pestifer* and other weeds form a fairly continuous cover over the short grass beneath.

The class 4 pasture had been subjected to heavy grazing for several years previous to 1940, and dusting from adjacent cultivated fields was extreme in 1935 and occasionally severe subsequently. As a consequence, the native vegetation had been practically destroyed. No native grasses were found in the areas marked for clipping. Weeds, however, were abundant. Large plants of *Salsola pestifer* 2 to 3 feet high, and 4 to 6 feet in diameter were common. The yield of weeds in 1940 was 2,700 pounds and in 1941 it was 2,010 pounds.

DIGHTON PASTURES

Class 1 pasture was composed of short grasses and weeds; here, as at Ness City, no mid grasses occurred in the clip quadrats (Fig. 22). The cover in 1940 was 10.9 percent and the yield was 106 pounds. In 1941, the cover had increased to 55.3 percent and the yield to 1,854 pounds. The yield of weeds, primarily *Lepidium densiflorum,* was 1,413 pounds in 1940, but only 108 in 1941.

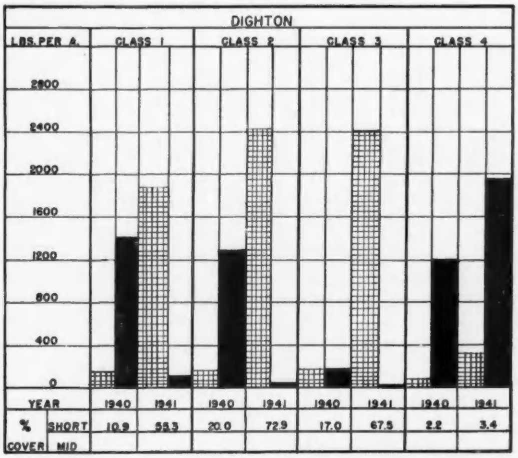

FIG. 22. Percentage basal cover and yield in pounds per acre of short grass (crosshatch) and weeds (black) at Dighton.

Class 2 pasture, with 20 percent cover, yielded 187 pounds of short grass in 1940. The next year the cover had increased to 72.9 percent and it yielded 2,412 pounds. The yield of weeds was 1,233 pounds the first year, but only 52 the second. Thus, while weeds were abundant at the preceding station, conditions for germination and establishment were poor here despite the presence of abundant seed.

Class 3 pasture had a cover of 17 percent in 1940 and yielded 184 pounds of short grass. The cover during the next year increased to 67.5 percent and yielded 2,401 pounds. The yield of weeds was almost negligible being 185 pounds in 1940 and 40 in 1941.

Class 4 pasture was grazed severely previous to 1935. The dusting from adacent cultivated fields was extremely severe during the spring and as a con-

sequence most of the vegetation was smothered. The cover of short grass in 1940 averaged only 2.2 percent, from which only 98 pounds were harvested. In 1941 it increased to 3.4 percent and the yield of short grass to 360 pounds. Weeds were abundant. Yields of 1,210 and 1,985 pounds, respectively, were obtained in 1940 and 1941.

Class 1 pasture at Phillipsburg (actually a drought- and dust-depleted mid-grass prairie) yielded 163 pounds per acre of short grass in 1940 from a cover of 4.8 percent.[5] The yield of mid grass, nearly all *Bouteloua curtipendula,* was only 14 pounds from .3 percent cover. In 1941 the cover of short grass had increased to 16.1 percent from which 709 pounds per acre were harvested. The yield of mid grass was 92 pounds from 1.2 percent cover. The yield of weeds, mostly *Lepidium densiflorum* and *Hordeum pusillum,* was 864 pounds per acre in 1940 but during the next year of more abundant rainfall 3,376 pounds.

Discussion

Examination of the data shows that there is only a general correlation between cover and yield. This is because of the great variability in vigor of the drought-stricken vegetation at the several stations and differences in degree of burial by dust in different pastures. This resulted in varying degrees of dormancy and protection from drought. Moreover, differences in time and amount of water available for growth prevented close agreement between amount of basal cover and yield. Some relationships, however, stand out plainly. During the good year of growth (1941) the weakened vegetation was greatly invigorated. But at both Hays and Ness City the production per unit of plant cover in class 1 and 2 pastures decreased compared with the yield in 1940 when the basal cover was much smaller (Table 3). In class 3 and 4 pastures where dusting had been heavy and the original cover very open, production per unit basal cover increased. At Ness City this increase was great.

At Quinter and Dighton there were increases in yield per unit percent of cover in all classes of pastures. Gains in classes 1 to 3 varied only from 21 to 32 pounds per unit of cover, except in class 2 at Quinter where the gain was only 13 pounds. The gain in the class 4 pasture was 61 pounds per unit of vegetation. Environmental conditions at these stations were less favorable to growth than those at Hays and Ness City in both 1939 and 1940. When the drought was finally broken in 1941, the cover increased rapidly and plant production per unit of cover was relatively high.

The basal area of sand dropseed is not considered in this comparison of cover and yield since this grass did not occur regularly, and especially because yield of this mid grass per unit of basal cover is usually several times that of either of the short grasses.

[5] This prairie was mowed annually except during the worst years of drought. Being unfenced, it was subjected to some grazing during winter.

TABLE 3. Percentage basal cover of short grasses, seasonal yields in pounds, and yields in pounds per one percent of cover.

	Hays			Ness City			Quinter			Dighton		
		Yield Pounds			Yield Pounds			Yield Pounds			Yield Pounds	
Class	Cover Percent	Total	Per 1 Percent Cover	Cover Percent	Total	Per 1 Percent Cover	Cover Percent	Total	Per 1 Percent Cover	Cover Percent	Total	Per 1 Percent Cover
						1940						
1	37.1	1,378	37.1	21.0	708	33.7	4.0	99	24.8	10.9	106	9.7
2	20.1	534	26.6	11.0	478	43.5	1.7	41	24.1	20.0	187	9.4
3	4.7	231	49.1	10.2	459	45.0	6.9	104	15.1	17.0	184	10.8
4	2.3	110	47.8	4.3	118	27.4	....	......	....	2.2	98	44.5
						1941						
1	95.6	1,524	15.9	45.0	1,390	30.9	23.7	1,081	45.6	55.3	1,854	33.5
2	42.8	902	21.7	42.6	1,610	37.8	18.5	686	37.1	72.9	2,412	33.1
3	21.7	1,170	53.9	49.6	2,810	56.7	32.0	1,511	47.2	67.5	2,401	35.6
4	22.6	1,092	48.3	22.0	752	34.2	....	......	....	3.4	360	105.9

The experimental data show the general trends in regard to the effects of drought, dust, and intensity of grazing on cover and yield. Where disturbance has been so widespread and the climatic conditions so erratic, certainly the more uniform results often obtained from a type of grassland of limited range and uniform past history and environment are not to be expected. It is believed, however, that this sampling of a number of apparently similar but widely separated pastures gives a better indication of the prevailing amount and development of the regional vegetation than could be had by more intensive studies on a single range.

A comparison of yields with those of similar vegetation under predrought precipitation is pertinent. Shantz (1911), working in eastern Colorado, calculated the yield of short-grass land from square yard areas. Late in August, 1909, it was 116 pounds per acre from ordinary cover and 400 pounds from an exceptionally thick one. Weaver (1924) secured the average air-dry weight of buffalo grass from a series of quadrats at Burlington, Colorado, and Phillipsburg, Kansas, during three growing seasons. In 1920, it was 874 and 2,587 pounds per acre at the two stations, respectively; in 1921, 1,846 and 2,373; and in 1922, 1,597 and 2,319 pounds in the same order. The data show that the yield is variable even during a series of good years. The amount of available soil moisture gives the explanation of the cause of the differences at the two stations and from year to year. Soil moisture was greater in amount and less often nonavailable for growth at the Kansas station.

In semiarid climates and especially during drought, amount and distribution of rainfall varies widely. Of no less importance is the manner in which rain falls and the cover and condition of the soil. A light rain on a soil with good cover may yield a greater water supply than a heavy one on bare or dust-covered land (Duley 1939; Duley & Kelly 1939).

In true prairie it has been shown that rainfall is absorbed approximately three times as fast where there is a stabilized cover of prairie grasses (Weaver 1942; Weaver & Albertson 1943).

Previous experience with drought and previous grazing treatments profoundly affect the vigor and future behavior of short grasses as does also a period of protection. The latter may have been furnished by partial burial by dust. It has been noted that a year of great vegetative activity of buffalo grass, as expressed in abundant stolon production, may be followed by one with much less vegetative increase. Nor is abundant tiller production compatible with the greatest yield of seed in blue grama.

Often the water, light, and nitrogen relations of the grasses were greatly affected by the growth of weeds. A survey of yield of weeds shows, however, that they occurred in large amounts (1,045 to 2,277 pounds) in all grades of pastures in 1940. Exceptions where they were fewer were class 1 and 2 pastures at Hays, class 2 at Dighton, and class 4 at Quinter. In 1941 weeds were again very abundant and nearly always occurred in larger amounts than in 1940 in 9 of the 16 pastures. They averaged far more abundant both years in class 4 pastures than elsewhere. Weeds, however, were not altogether harmful since upon their death they formed a mulch which protected the soil from violent impact of water. The growth and decay of their roots made compacted soil more porous and thus aided infiltration and indirectly promoted growth of perennial grasses.

MONTHLY YIELD OF NATIVE GRASSES

Previous observations and experiments had shown clearly that the growth and yield of the native grasses varied greatly not only from season to season but also from month to month (Weaver & Albertson 1943). Therefore an experimental study was made on monthly yields to ascertain variations in the amount and the causes of the fluctuations. Quadrats were clipped in each of the four classes of pastures at the four stations.

The quadrats were marked out in the spring of 1940. Ten were staked in each exclosure where the preceding quadrats were located. The yield was obtained at the end of each month from May to August, inclusive. Short grass, mid grass, and weeds were air-dried and weighed separately and the yields expressed in pounds per acre. Monthly precipitation at each station during the growing season is shown in Figure 7, and available soil moisture at Hays and Dighton in Figures 9 and 10. It should be emphasized that the extended drought in the fall of 1939 weakened the perennial grasses to such a degree that growth was resumed very late in 1940. Hence, the only vegetation harvested in May was the crop of annual weeds, mostly *Lepidium densiflorum, Lappula occidentalis, Monolepis nuttalliana,* and *Hordeum pusillum.*

The total monthly yields of perennial grasses and, in certain pastures, the monthly yields of short grasses are shown by means of graphs in Figure 23. At Hays the total grass produced during June, 1940 on the class 1 pasture was 416 pounds. During July production decreased to 366 pounds but increased to 596 during August. The yield in 1941 was in reverse order. The greatest amount, 750 pounds, was harvested at the end of May when the buffalo grass was heavily laden with seed. The staminate flowers extended a few inches above the semidecumbent leaves, and produced a characteristic spotted appearance of the landscape so common when this grass is in full bloom. Yield decreased to 431 pounds in June and to 95 in July. That of August was only 86 pounds.

Yields in the class 2 pasture followed somewhat the same trends as the preceding but were signifi-

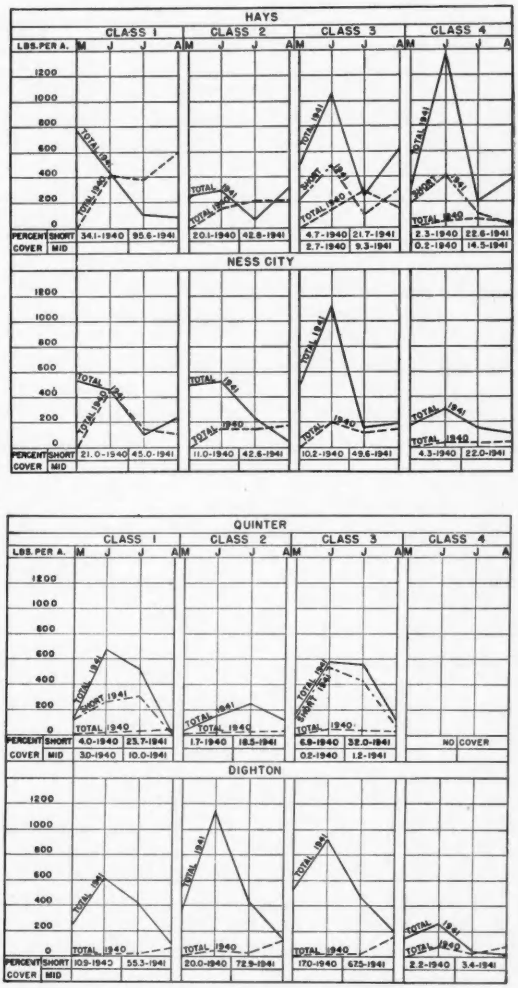

FIG. 23. Yields in May, June, July, and August in different classes of pastures in 1940 and 1941 at each of the four stations. The percentage of basal cover of short grasses and mid grasses is also given for each pasture.

cantly lower. The short grasses were so badly damaged by drought and competition with little barley both seasons that the yields were low. The total grass produced during June, 1940 was 150 pounds. Yield increased to 185 pounds in July, and to 199 in August. In 1941 competition with little barley was intense during late spring and the yield in May was only 240 pounds. It was slightly greater, 290 pounds, in June. Drought during July reduced the yield to only 55 pounds but in August it was 265.

Total yield in 1940 on the badly dusted and heavily grazed class 3 pasture, with a cover of only 7.4 percent, increased from zero in May to 306 pounds in July. In August it was only 146 pounds. The low yield in 1940 resulted from feeble growth of the drought-stricken vegetation. Excellent growing conditions in the spring of 1941 resulted in vigorous growth of both short and mid grasses. The short-grass yield in May was 221 pounds but this increased to 519 in June. The July harvest yielded only 113 pounds. This low yield, however, was offset by one of 318 pounds in the wet month of August. The difference between the short-grass yield and the total yield represents the production of mid grasses, mostly *Sporobolus cryptandrus*. During May the yield of mid grass was 262 pounds and in June and July 531 and 143 pounds, respectively. The yield in August was 290 pounds. Rapid recovery of the vegetation of this and other badly damaged areas was probably due to accumulation of fertile soil from dusting, and semi-dormancy through much of the drought period.

Total yield of grasses in class 4 pasture in 1940 was much less than that in class 3. The total amount of short and mid grasses produced in June was only 22 pounds. In July it was 59 pounds and in August 51. The cover of short grass increased to 22.6 percent in 1941 and the yield in May was 192 pounds. Production increased to 426 pounds in June and then declined to 97 and 38 pounds, respectively, in July and August. The mid grass grew vigorously in 1941 and in fall had a basal cover of 14.5 percent. The yield in May was only 78 pounds. In June, however, it reached a value of 959 pounds which, with the short grass, exceeded the yield of all the higher classes of pastures (Fig. 23). A yield of only 98 pounds in July resulted from a drought of short duration; in August, it was 320 pounds.

Yield at Ness City in 1940 was relatively high in June in class 1 pasture but low thereafter. It was uniformly low in the other three classes (Fig. 23). Extremely low yields were produced in all pastures at Quinter in 1940, since the vegetation was sparse and had scarcely recovered from the extremely severe drought of the previous fall. There was some yield at the end of May, 1941, good yields in pasture classes 1 and 3 in June and July, but they were low following the August drought. At Dighton in 1940, low monthly yields were secured, with an increase in growth in August. Conversely, the yields even in May, 1941, were good at all stations and those of June were excellent. They were obtained from a vigorous, rapidly increasing cover, with the exception of class 4 pasture.

DISCUSSION

Variability in productivity was due in part to uneven distribution of precipitation but also to the previous experience of the vegetation especially as regards drought, dusting, and intensity of grazing. The very low yields at the two westerly stations, Quinter and Dighton, in 1940 are attributed to two factors—the extremely severe drought that prevailed there during the preceding fall and winter and the low precipitation and small amount of available water in 1940. Rainfall in the spring at these stations was lower than at the others (except Hays in May) and did not promote much growth (Fig. 7). Low precipitation would account for the depressed yield in June and July, but the vegetation at neither station responded favorably to the 2.5 to 4 inches of rainfall and good water content of soil during August (Figs. 7 and 10). The late resumption of growth in 1940 at Hays and Ness City was also an after-effect of the fall drought of the preceding year. The greater yield at Hays in class 1 pasture than in the others is explained on the basis of a more rapidly extending and more vigorous cover. While this denser vegetation was undoubtedly exhausting available soil moisture more rapidly than the more scattered plants in the other pastures, the very presence of the cover greatly promoted water infiltration and thus compensated this loss. Moreover, there were more early growing, water dissipating, annual weeds where the perennial grasses were sparse.

In 1941 the heaviest monthly yields occurred in May in class 1 pastures at Hays and Ness City but a month later in the other class 1 pastures. Precipitation was somewhat higher at Hays and Ness City (Fig. 7) and the soil at Hays had much more water available for growth than that at Dighton (Figs. 9 and 10). Moreover, the vegetation seemed much more vigorous at the stations where growth was earlier. Decrease in monthly productivity after the high early yields was undoubtedly due in part to continuous clipping (Weaver & Hougen, 1939). A very dry July followed by a wet August at Hays accounts for the upward trend of the graph of production at this station. From the excellent yield in class 3 and 4 pastures it would seem that dusting stimulated growth under good precipitation, also in both pastures high-yielding mid grasses were present. The same effect is evident in class 3 pasture at Ness City where mid grasses were not found. Growth in the several pastures at Quinter showed rather uniform monthly trends. Less than an inch of rainfall in August resulted in little development in late summer. At Dighton the yields in all pastures directly reflect the rainfall of June, July, and August which was about 5, 4.5, and 2 inches, respectively. Decrease in monthly productivity was similar in pastures with only 3 percent basal cover to those with 55 to 73 percent. Here weeds grew in numbers and stature somewhat in inverse proportion to the amount of perennial grasses.

Blue grama and buffalo grass have a remarkable capacity, except immediately after extremely severe and prolonged drought, to revive quickly and grow rapidly at any time during the warm season and to become dormant but remain alive when available soil moisture is exhausted. This is in accord with their semiarid environment and normally occurs every year. During a drought year it may take place several times. But when the spark of life is nearly extinguished, as in 1939, recovery is slow. The difference between total denudation and relict vegetation over thousands of square miles depended upon the wonderful drought resistance of these two species. They remained where all other perennial vegetation vanished. Sand dropseed, also very drought resistant and likewise with remarkable powers of recuperation, has spread widely on the bare, dry, warm soils in the past five years.

Revegetation of the central Great Plains area depends in the main upon the growth and spread of these xeric but nutritious grasses. These data show clearly their ability, once established, to increase their area. Buffalo grass alone can spread with great rapidity. Blue grama and sand dropseed increase much more slowly and must have good years for seed production followed by favorable years for seedling establishment (Weaver & Mueller 1942). Although the cover may increase fourfold in a single year, which is an unusual gain, on the thousands of ranges where it was only 2 to 5 percent (Weaver & Albertson 1940a) this process must be repeated several times before the cover is completely restored. A series of good years are necessary for restoration of a plant matrix as dense as that which prevailed before the drought. It will not occur quickly. Succession even in subseres proceeds slowly and weeds will play their inevitable and important part (Clements 1916, 1929). The more serious the degeneration the longer will be the period of redevelopment. Upon the revegetation of the range depends the fundamental economy of the Great Plains (Clements & Chaney 1937). Retardation of recovery by injudicious grazing must be carefully avoided; cropping practices must be such as to stabilize plowed land and prevent soil from being carried away as dust; and the best principles of ecological and agronomic practices must be used in reclothing marginal lands with grass and restoring a normal cover to depleted ranges (Savage 1939; Savage & Runyon 1937).

EFFECTS OF DIFFERENT INTENSITIES OF CLIPPING ON YIELD

An understanding of the relationship of plant productivity to intensity of grazing is very important. In order to secure information on this phase of range conservation as applied to short grasses, selected areas were clipped at different intervals and the yields determined. The experiments were done at all four stations, four classes of pastures being used at each station. In each of the 16 pastures, the four areas used were closely adjacent and had received the same treatment as regards the amount of grazing, severity of drought, and deposition of dust previous to 1940, when the study was begun. A total of nearly 40 meter quadrats was employed in each pasture, approximately 10 under each of the four different treatments. The intensity of clipping for each of the four treatments was as follows:

1. Clipped monthly from May to August, inclusive, in 1940 and 1941.
2. Clipped monthly as above in 1940, but clipping deferred until the end of the season in 1941.
3. Unclipped in 1940; clipped monthly in 1941.
4. Unclipped in 1940; clipping deferred until the end of the season in 1941.

The area of the basal cover in the fall of 1941, when the quadrats were charted, was approximately the same under treatments 1 and 2. It was likewise practically the same under treatments 3 and 4. The basal cover of short grass and mid grass is given, therefore, as the average of conditions 1 and 2, and 3 and 4 in each class of pasture, respectively (Fig. 24). It is significant, however, that the total cover ranged from 2 to 4 percent greater under treatments 3 and 4.

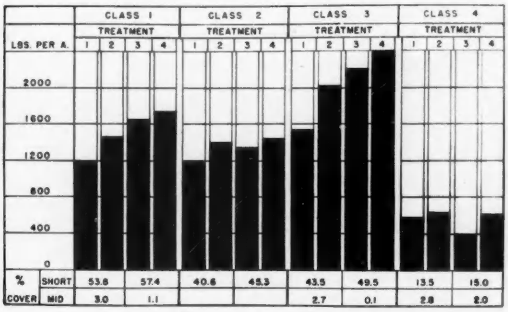

FIG. 24. Average basal cover and yield in pounds per acre in 1941 of short grass in each class of pasture when clipped monthly in 1940 and 1941 (treatment 1), when clipped monthly in 1940 but only in fall in 1941 (treatment 2), when unclipped in 1940 but clipped monthly in 1941 (treatment 3), and when unclipped until the fall of 1941 (treatment 4).

Yield of short grasses, with one exception, was greatest under treatment 4 and least under 1 (Fig. 24). This indicates that close clipping of short grass for two seasons tended to reduce the yield and that each of the other treatments were, in order, nearly always less detrimental. In class 1 pastures for example, the average yield of short grass was 1,182 pounds per acre. Under treatment 2 it was 1,463 pounds or nearly 300 pounds per acre greater than under monthly clipping. Under treatment 3 the yield was further increased to 1,624 pounds. The greatest yield was 1,681 pounds per acre in the pasture which had two years of rest (treatment 4). The yield of class 2 pastures was somewhat less than that of class 1, but, with one minor exception, it varied in the same sequence. Under treatments 1 to 4 yields were

1,203, 1,400, 1,390, and 1,470 pounds per acre, respectively.

Yields of class 3 pastures consistently increased from treatments 1 to 4. They were also greater for each treatment than the corresponding yield in classes 1 and 2. Under treatment 1, the production of short grass was 1,560 pounds per acre. It was 2,042 pounds under treatment 2, and 2,284 and 2,400, respectively, under treatments 3 and 4.

The short grass in class 4 pastures was doubtless affected less by intensity of clipping than by competition of annual weeds. Yields were therefore not consistent. From treatments 1 to 4, in order, they were 575, 624, 370, and 593 pounds per acre.

The yield of mid grasses, mostly *Sporobolus cryptandrus,* was always greater under the second treatment than the first, and usually greater under the fourth than the third. This indicates that monthly clipping greatly reduced growth and yield. The presence of sand dropseed usually indicated a broken cover in the original short grass. Its rate of growth varied greatly. For example, in the class 3 pastures, the yield varied from 0 to 400 pounds per acre in 1941.

The effect of intensity of clipping upon the monthly and seasonal yield in 1941 in representative class 1 and class 3 pastures is given in Table 4. The yield of short grass in the class 1 pasture under the first treatment was 1,362 pounds per acre. Under treatments 2, 3, and 4 it was 1,524, 1,976, and 2,185 pounds per acre, respectively. The monthly yield for the same year was significantly greater under treatment 3 than under 1. In May it was 1,216 pounds per acre as compared with 750 pounds under treatment 1. In the same sequence, it was 462 and 431 pounds in June, 167 and 95 in July, and 129 and 86 in August. Under both treatments, the yields were greatest in May and gradually decreased thereafter.

TABLE 4. Yields in pounds per acre of short grasses in 1941 in representative class 1 and class 3 pastures under different intensities of clipping.

Station	Class	Treatment	Yields by Months				
			May	June	July	August	Total
Hays	1	1	750	431	95	86	1,362
		2	.....	...	...	1,524	1,524
		3	1,216	462	167	129	1,976
		4	.....	...	...	2,185	2,185
Quinter	3	1	147	542	473	73	1,235
		2	.....	...	...	1,511	1,511
		3	125	596	697	200	1,620
		4	.....	...	...	1,947	1,947

The seasonal yield in class 3 pasture under treatment 1 was 1,235 pounds (Table 4). Under succeeding treatments it increased to 1,511, 1,620, and 1,947 pounds, respectively. Moreover, the yield, as in the class 1 pasture, was greater each month, except May, in the pastures under the third treatment than under the first. The lower yield in May may be attributed to less cover here than in the class 1 pasture in spring, since the increase in cover was extremely rapid. The dry August limited the yield of short grasses to 73 pounds under the first treatment but 200 under the third.

Discussion

Grazing, or clipping to simulate grazing, is a more or less destructive process since it removes much of the photosynthetic area from the plant. Preservation of pasture grasses depends upon manufacture and storage of foods by the plants in excess of those consumed in growth. Whenever grazing is so intensive that it permits complete and frequent removal of the green shoots it greatly reduces the manufacture of carbohydrates and prevents their storage in underground parts. Such abrupt decrease in photosynthetic activity causes a corresponding decrease in the growth of roots. Continued defoliation is extremely injurious and unless reasonable precautions are taken to prevent it the effects are likely to become cumulative and cause serious deterioration of pasture or range. This may be followed by erosion, loss of nutrients, and general impoverishment of the soil.

Canfield (1939) found that quadrats of black grama *(Bouteloua eriopoda)* clipped periodically during the growing season to a height of one inch made substantial gains in tuft areas the first year, one of unusually favorable growth, but these gains were temporary. Losses in the second and third year were greater than these gains, and losses continued to the end of the experiment. Similar results were obtained where the clipping was 2 inches high.

Results from studies on the effects of the removal of the photosynthetic area are in agreement that the yield and vigor of the vegetation vary inversely with the frequency of clipping. Aldous (1930) applied clipping treatments at two-week intervals to prairie grasses (chiefly big and little bluestems) at Manhattan, Kansas. He found that the density of the vegetation decreased about 60 percent in three seasons. Clipping at three-week intervals resulted in only 13 percent reduction. Disappearance of valuable species was proportional to frequency of cutting. The higher nutritive value of the forage gained from frequent harvesting did not compensate the loss in yield.

Total yields of quadrats clipped at frequent intervals at Lincoln, Nebraska, exceeded the single yield of the control of *Andropogon scoparius* by 11 and 26 percent during two seasons, respectively. Similar yields of *Bouteloua gracilis* on upland were 6 percent greater than the control and 30 percent greater on lowland. *Poa pratensis* when frequently clipped exceeded the control in yield by 5 percent. This increased growth is made at the expense of accumulated reserves in the roots and crown. The first growth following defoliation is largely "transfer growth" from storage tissue to herbage. It results in decreasing the vigor of the plant. Thus, the greater frequency of removing the top either by clipping or grazing at first results in greater yield of dry matter, but only until a point is reached where

the defoliation is so frequent as to prevent the rebuilding of root reserves.

Quadrats frequently clipped during a second season always gave lower yields than a single clipping of the controls. In little bluestem the yield averaged 46 and 49 percent less, in big bluestem 28 percent, and in mixed little and big bluestem 43 and 53 percent less than the control. Yields of quadrats frequently clipped during two years were likewise much lower than those similarly clipped for only a single year. In little bluestem, the former yielded 60 percent less, in big bluestem 37, and in mixed bluestems 51 percent. Yields were still further reduced where clipping was continued a third season. Compared with controls they were 56 to 68 percent less, respectively, in little bluestem and mixed-bluestem types. Moreover, when these yields were compared with those from quadrats frequently clipped for two years, they were found to be 42 and 23 percent less, respectively (Weaver & Hougen 1939). Thus, there is a rapid decrease in yield following too close utilization of a pasture.

McCarty (1938) has shown that the "initial growth of herbage in spring is made at the expense of the carbohydrate accumulations stored in the basal organs during the preceding season. Concentration of carbohydrates in both herbage and basal organs of the plant is inversely related to the rate of herbage growth. This relationship is maintained throughout the entire annual cycle of growth. The accumulation of carbohydrates stores is delayed, therefore, until most of the annual herbage growth is produced." It is well known that all of the stored food is not ordinarily used in normal early growth of perennial grasses. But if the new growth is removed by early grazing or clipping there results a diminution in the reserve food: a second close clipping may further deplete the supply. Thus, the progressive increase in yield of the closely clipped quadrats and the final death of many plants may be readily understood. Mixed prairie, for example, in past decades has lost much in its forage production in being reduced to the short grass disclimax. Where upland, little bluestem degenerated into pasture of the short-grass type at Lincoln, Nebraska, the seasonal yield was reduced about half.

Biswell and Weaver (1933) found not only that the total dry weight produced from sods frequently clipped after transplanting ranged from 13 to 47 percent of that of the same species of prairie grass unclipped after transplanting but also that the clipped plants failed to produce new rhizomes and many of the old ones died. The length of the roots was greatly decreased, and the relative production of roots was more greatly reduced than that of tops. Plants weakened by repeated clipping renewed growth slowly if at all after the sods were frozen, although the controls made an excellent development. They give a comprehensive review of the literature.

Robertson (1933) has shown the very detrimental effects of removing the tops of seedling grasses upon the growth of both tops and roots.

The farmer's experience in recent times has made him well aware of the importance of good pastures for feed during severe drought, for preventing damage from wind erosion, and for combatting damage by floods which often follow prolonged drought. A great problem lies in adjusting livestock to the carrying capacity of the range. The false creed that profits depend on livestock numbers must be replaced by the viewpoint that native vegetation is a perennial crop and that next year's yields may be lessened somewhat in proportion to the extent of this year's grazing and trampling. It is only slowly being realized that larger immediate returns, to say nothing of future yields, from the midwestern ranges can be obtained from moderate stocking than from overgrazing. Man has under his control the season of grazing, the frequency of removal of the new growth of grasses, and how closely they are grazed. While he cannot prevent droughts he can keep the ranges in good condition to endure them.

SUMMARY

The very extensive range lands of western Kansas are now recovering from the extremely damaging effects of drought and burial under dust. Those that were most judiciously grazed before and during the dry cycle and best protected from dust accumulation, either by large size or by stabilizing nearby tilled land, usually suffered the least degeneration.

At four widely separated stations, Hays, Ness City, Dighton, and Quinter, pastures were selected for study at the end of the most severe drought ever recorded. Four classes of pastures were investigated at each station where the range use was known or where records were obtained. Class 1 had been lightly grazed and lightly dusted, class 2 heavily grazed and lightly dusted, class 3 lightly grazed but heavily dusted, and class 4 both heavily grazed and heavily dusted. A prairie at Phillipsburg had degenerated like the preceding to short grass but only because of drought.

A record of annual and monthly precipitation was obtained for each station, available soil water to 5 feet in depth was ascertained monthly during the growing season, and other environmental factors were studied in 1939, 1940, and 1941.

Increase in basal area of perennial grasses, amount of the various species concerned, and dry weight of forage produced were the chief criteria used in measuring recovery. Exclosures against stock were made. In each exclosure 20 meter quadrats were clipped annually and the basal area of the perennial grasses charted by means of a pantograph in 1940 and 1941. Blue grama *(Bouteloua gracilis)* and buffalo grass *(Buchloe dactyloides)*, both short grasses, composed the bulk of the scanty, relict perennial vegetation. Sand dropseed *(Sporobolus cryptandrus)*, which occurred irregularly and sparingly, was practically the only mid grass. Native forbs were so few as to be almost negligible but annual weeds were abundant. Increase or decrease of

basal area of each species of grass was ascertained, and the separate yields of short grasses, mid grasses, and weeds were obtained.

Low precipitation in 1939, 7 to 10 inches below the normal 19 to 23 inches, and extremely dry fall further reduced the much depleted plant cover. Drought also weakened the vegetation so greatly that it remained almost dormant at all stations the following spring, and nearly throughout the summer at Dighton and Quinter.

The growing season of 1940 showed much improvement over that of 1939, but precipitation was below normal at all stations during April and June. At Hays and Ness City only was the amount of precipitation normal. Despite the moderate rainfall, the thoroughly dried soil was often without available water at all stations and growth was not continuous nor yields high, except those of annual weeds.

In 1941 the rainfall was above normal more than half of the time from April to September. The soil was wet from early spring until July; periods without rain were not prolonged and not severe, and the drought was definitely broken.

Basal area, first determined in the fall of 1940 after a year of recovery, showed that the cover was invariably least in all class 4 pastures at any station, and nearly always highest in class 1. Cover in pasture classes 2 and 3 was intermediate, but often higher in the lightly grazed but heavily dusted class 3. A light cover of dust often furnished some protection against drought by aiding dormancy. The average basal cover of short grasses in the four class 1 pastures was 18 percent; that in the others in order 13.7, 13.4, and 2.2 percent. During the excellent season for growth in 1941 these pastures extended their basal cover to 56.8, 46.3, 44.3, and 17.2 percent, respectively. Thus, classes 1 to 3 on an average tripled their cover; that in class 4 increased nearly eightfold.

Blue grama exceeded buffalo grass in amount of basal area in all but two class 1 and 2 pastures. But at the end of 1941 buffalo grass exceeded blue grama in basal area in 7 of these 8 pastures. There was about 4.5 times as much buffalo grass as blue grama in the average of class 1 pastures, and about 3 times as much in the average of class 2. In the heavily dusted pastures (classes 3 and 4) in 1940, buffalo grass ranked somewhat higher in all except 2, but percentage of cover was low. In 1941, so great were its gains, it ranked far ahead of blue grama, often being 3 to 5 times as abundant. In the few pastures where sand dropseed occurred it increased rapidly but seldom composed more than a small part of the vegetation. Despite fourfold increases of cover in low grade pastures, several good years for seed production and growth of seedlings will be required for complete restoration of the cover.

Only broad correlations were found between amount of basal cover and yield, the drought-stricken vegetation varied greatly in vigor; the amount of dust accumulation resulted in varying degrees of dormancy and protection from drought. Moreover, occurrence and amount of soil moisture available to growth was extremely variable.

During 1941 an abundance of water greatly invigorated the weakened short grasses at Hays and Ness City. But where increases of the moderately small cover in the best pastures had been high in 1940, seasonal yield in relation to amount of cover was less in 1941. The decrease was from 27-44 pounds per acre for 1 percent basal cover in 1940 to 16-38 pounds in 1941. But where dusting had been heavy and the original cover very open at these stations, production per unit of basal cover increased in 1941, often greatly.

At Quinter and Dighton conditions were unfavorable to growth in 1940 and yield per unit of cover was low, 10 to 25 pounds per 1 percent of cover per acre. It increased, with one exception, 21 to 32 pounds per unit cover in 1941 over that in 1940. Where the initial cover was least (about 2 percent) and dusting greatest (class 4 pastures) the yield was even more greatly increased.

Cover of sand dropseed is not included in preceding statements of yields since its yield per unit of cover is usually several times as great as that of short grasses.

These short-grass yields were mostly far below those made at Phillipsburg during the years of more nearly normal precipitation, 1920, 1921, and 1922. Only in one pasture at Ness City and at Dighton where the basal cover was about 70 percent was this average yield, 2,400 pounds per acre, attained even during the wet year, 1941.

In many pastures both spread and yield of the perennial grasses were greatly reduced by an abundance of weeds, chiefly *Hordeum pusillum, Lepidium densiflorum, Chenopodium album,* and *Salsola pestifer.* They absorbed much water, and greatly reduced the light both when living and dead. They were most abundant in class 4 pastures. Weeds usually yielded one-fourth ton to more than one ton per acre.

Monthly yields were obtained from a series of 10 quadrats in each of four classes of pastures at the four stations. Great variability in monthly yield resulted from uneven distribution of precipitation and previous experience of the vegetation as regards drought, dusting, and intensity of grazing.

Yields in 1940 were extremely low at Quinter and Dighton where previous drought had been most severe. At Hays and Ness City there was no yield in any pasture in May, but moderate yields each summer month thereafter, except in class 4 pastures.

The highest or next to the highest monthly yields in 1941 occurred in May in class 1 and 2 pastures at Hays and Ness City, but after May or June yields decreased sharply. But in class 3 and 4 pastures they were the greatest in June, the June yield usually far exceeding that in the class 1 and 2 pastures. Excellent yields from a rapidly increasing cover occurred in 1941 at Quinter and Dighton where they were high in May but highest in June, and low

following the August drought. Early growing, water dissipating, annual weeds often reduced the May yield of perennial grasses.

In order to determine the effects of different intensities of clipping on yield, grasses were (1) clipped monthly in 1940 and 1941, (2) clipped monthly in 1940 but only in fall in 1941, (3) unclipped in 1940 but clipped monthly in 1941, and (4) unclipped until the fall of 1941. These 4 treatments were applied in class 1 to 4 pastures at both Hays and Quinter. The cover was approximately the same in the fall of 1941 under treatments 1 and 2, but 2 to 4 percent higher, although similar under treatments 3 and 4.

In class 1 pastures the average yield of short grass was 1,182 pounds per acre under treatment 1; under treatments 2 to 4 it was 1,463, 1,624, and 1,681 pounds, respectively. A sequence of increasing yields was also obtained in class 2 and 3 pastures, the class 3 pasture giving greater yields under each treatment than pasture classes 1 and 2. In class 4 pastures the short grasses were affected less by intensities of clipping than by competition of weeds.

LITERATURE CITED

Albertson, F. W. 1937. Ecology of mixed prairie in west central Kansas. Ecol. Monog. **7**: 481-547.

1938. Prairie studies in west central Kansas. Kan. Acad. Sci. Trans. **41**: 77-83.

1939. Prairie studies in west central Kansas. Kan. Acad. Sci. Trans. **42**: 97-107.

1941. Prairie studies in west central Kansas. Kan. Acad. Sci. Trans. **44**: 48-57.

Albertson, F. W., & J. E. Weaver. 1942. History of the native vegetation of western Kansas during seven years of continuous drought. Ecol. Monog. **12**: 23-51.

Aldous, A. E. 1930. Effect of different clipping treatments on the yield and vigor of prairie grass vegetation. Ecology **11**: 752-759.

Biswell, H. H., & J. E. Weaver. 1933. Effect of frequent clipping on the development of roots and tops of grasses in prairie sod. Ecology **14**: 368-390.

Canfield, R. H. 1939. The effect of intensity and frequency of clipping on density and yield of black grama and tobosa grass. U. S. Dept. Agr. Tech. Bul. 681.

Clements, F. E. 1916. Plant succession. Carnegie Inst. Wash. Pub. 242.

1929. Climatic cycles and changes of vegetation. Rept. Conf. Cycles Carnegie Inst. Wash. **3-4**: 64-71.

Clements, F. E., & R. W. Chaney. 1937. Environment and life in the Great Plains. Carnegie Inst. Wash. Suppl. Pub. 24.

Culley, M. J., R. S. Campbell, & R. H. Canfield. 1933. Values and limitations of clipped quadrats. Ecology **14**: 35-39.

Donald, C. M. 1941. Pastures and pasture research. Six lectures delivered at the University of Sydney, 1941. Univ. Sydney.

Duley, F. L. 1939. Surface factors affecting the rate of intake of water by soils. Soil Sci. Soc. Amer. Proc. **4**: 60-64.

Duley, F. L., & L. L. Kelly. 1939. Effect of soil type, slope, and surface conditions on intake of water. Neb. Agr. Col. Exp. Sta. Res. Bul. 112.

Hanson, H. C. 1938. Ecology of grassland. Bot. Rev. **4**: 51-82.

Hein, M. A., & P. R. Henson. 1942. Comparison of the effect of clipping and grazing treatments on the botanical composition of permanent pasture mixtures. Jour. Amer. Soc. Agron. **34**: 566-573.

McCarty, E. C. 1938. The relation of growth to the varying carbohydrate content in mountain brome. U. S. Dept. Agr. Tech. Bul. 598.

Mueller, I. M., & J. E. Weaver. 1942. Relative drought resistance of seedlings of dominant prairie grasses. Ecology **23**: 387-398.

Robertson, J. H. 1933. Effect of frequent clipping on the development of certain grass seedlings. Plant Physiol. **8**: 425-447.

Sampson, A. W. 1914. Natural revegetation of range lands based upon growth requirements and life history of the vegetation. Jour. Agr. Res. **3**: 93-147.

Sarvis, J. T. 1923. Effects of different systems and intensities of grazing upon the native vegetation at the northern Great Plains field station. U. S. Dept. Agr. Bul. 1170.

Savage, D. A. 1937. Drought survival of native grass species in the central and southern Great Plains, 1935. U. S. Dept. Agr. Tech. Bul. 549.

1939. Grass culture and range improvement in the central and southern Great Plains. U. S. Dept. Agr. Cir. 491.

Savage, D. A., & H. E. Runyon. 1937. Natural revegetation of abandoned farm land in the central and southern Great Plains. Internatl. Grassland Cong., Aberystwyth, Gt. Brit., Rept. Sec. 1. Grassland Ecology, pp. 178-182.

Shantz, H. L. 1911. Natural vegetation as an indicator of the capabilities of land for crop production in the Great Plains area. U. S. Dept. Agr. Bur. Plant Ind. Bul. 201.

Taylor, W. P., & J. V. G. Loftfield. 1924. Damage to range grasses by the Zuni prairie dog. U. S. Dept. Agr. Bul. 1227.

Weaver, J. E. 1924. Plant production as a measure of environment. A study in crop ecology. Jour. Ecol. **12**: 205-237.

1942. Competition of western wheat grass with relict vegetation of prairie. Amer. Jour. Bot. **29**: 366-372.

Weaver, J. E., & F. W. Albertson. 1936. Effects of the great drought on the prairies of Iowa, Nebraksa, and Kansas. Ecology **17**: 567-639.

1940. Deterioration of grassland from stability to denudation with decrease in soil moisture. Bot. Gaz. **101**: 598-624.

1940a. Deterioration of midwestern ranges. Ecology **21**: 216-236.

1943. Resurvey of grasses, forbs, and underground plant parts at the end of the great drought. Ecol. Monog. **13**: 63-117.

Weaver, J. E., & V. H. Hougen. 1939. Effect of frequent clipping on plant production in prairie and pasture. Amer. Mid. Nat. **21**: 396-414.

Weaver, J. E., & I. M. Mueller. 1942. Role of seedlings in recovery of midwestern ranges from drought. Ecology **23**: 275-294.

West, C., G. E. Briggs, & F. Kidd. 1920. Methods and significant relations in the quantitative analysis of plant growth. New Phytol. **19**: 200-207.

West, O. 1936. An investigation of the methods of botanical analysis of pasture. South African Jour. Sci. **33**: 501-559.

ECOLOGICAL STUDIES OF SESSILE ROTATORIA

PART I. FACTORS AFFECTING DISTRIBUTION

W. T. Edmondson

Naval Research Assistant to the Director, American Museum Natural History, New York City

Based on part of a dissertation submitted to Yale University in partial fulfilment of the requirements for the degree of Doctor of Philosophy. Contribution from the Osborn Zoological Laboratory.

TABLE OF CONTENTS

	PAGE
Introduction	33
The Effect of the Chemical Nature of Water	33
The Effect of the Substrate	33
The Relation to Surface as Such	34
Acknowledgments	35
The Sessile Rotatoria	35
Taxonomy and Life History	35
Material and Methods	36
The Association of Species	36
Factors Affecting the Distribution of Sessile Rotatoria	39
Hydrogen Ion	40
Bicarbonate	41
Calcium	42
Magnesium	42
Conductivity	42
Other Factors	43
Discussion	43
The Relationship between Sessile Rotatoria and Their Substrate	44
The Effect of Surface as Such	44
Factors Which Affect the Distribution of Substrate Plants	45
The Attachment of Rotatoria to Plants	46
The Fauna of Different Plants	47
Frequency of Attachment to Substrates: Specific Analysis	50
Experimental Analysis	54
Optimal Substrates	58
The Effect of Plant Succession on the Rotifer Fauna	58
The Effect of Habitat Size on the Rotifer Fauna	59
Regional Differences in the Fauna	61
General Discussion	62
Geographical Distribution	62
Environmental Limitations	63
Local Distribution in Lakes	63
Summary	64
References	64

ECOLOGICAL STUDIES OF SESSILE ROTATORIA

PART I. FACTORS AFFECTING DISTRIBUTION

INTRODUCTION

Ever since the discovery of *Limnias ceratophylli* and *Floscularia ringens* by Leeuwenhoek in 1703, sessile Rotatoria have received considerable attention, particularly from taxonomists. Yet the last major taxonomic contribution was made more than thirty years ago, and there has never been a serious attempt to study any aspect of the ecology of the group. The present studies represent such an attempt, and although limited to the sessile Rotatoria, are intended as a contribution to the more general literature of the periphyton.

The terminology applied to various kinds of growths of sessile organisms has been reviewed by Roll (1939), who is followed here; periphyton consists of all sessile organisms on any substrate. The periphyton can be divided into two groups on the basis of the inter-relationship of the component organisms. Epiphyton is the totality of sessile organisms which are not associated in a mechanical sense; they are separated from each other. Lasion consists of organisms which are associated mechanically and apparently have a direct influence on each other; they form a layer over the surface of a substrate bounded on the outer side by free water and loosely enclosing spaces of various sizes, thus forming a biotope for associated, non-sessile organisms. Meuche (1939) characterized a number of types of periphyton by the nature of the sessile organisms that compose them. As the present author understands and uses the term, periphyton is a general term that refers only to sessile organisms whether they be plant or animal. The huge fauna of free-swimming organisms which lives in the lasion (Meuche 1939) is not a part of the lasion, but is simply associated with it in much the same way that birds are associated with a forest. Young (1941) has discussed the most important works dealing with the periphyton, and it is needless to repeat such a discussion here. It will be of value to outline the scope of the present paper with reference to past studies as a background.

The Effect of the Chemical Nature of Water

If any of the component organisms of the periphyton is sensitive to chemical and physical differences in water, the character of the periphyton must be varied in different types of water, so far as the presence or absence of the sensitive species is concerned. The present paper is largely devoted to such effects. A large literature exists with data on the ranges of tolerance of a great number of organisms, much of it concerning the effect of pH as an effective factor in limiting distribution of organisms. No review of this literature is possible here, but some of the papers with data on factors affecting the distribution of small, fresh water animals are listed: Protozoa, Noland (1925), Lackey (1938), Saunders (1924), Darby (1929); Sponges, Jewell (1935, 1939); Nematodes, Schneider (1937); Bryozoa, Brown (1933); Mollusca, Morrison (1932); Rotatoria, Harring & Myers (1929), Myers (1931, 1937, 1940, 1942), Hauer (1937-38), Ahlstrom (1933), Edmondson & Hutchinson (1934); miscellaneous organisms, Skadowsky (1923), Ward (1940), Reif (1940), Rudolfs & Lackey (1929), Hutchinson, Pickford & Schuurman (1932), Yoshimura (1933).

Many of the papers cited show that the fauna can often be correlated with the chemical nature of the habitats, some species, for instance, being found only in acid waters, others in alkaline waters. In all the cases, however, it is very difficult to decide just which factors are those actually effective in limiting distribution of organisms. For example, a low pH is usually associated with a low concentration of bicarbonates, and likewise, hard waters are usually alkaline. In order to separate the effects of correlated variables, both experimental work and extensive observation of natural habitats are needed. From results of certain experiments Jewell (1939) concluded that calcium bicarbonate rather than pH is the effective factor in limiting the distribution of some fresh water sponges.

The Effect of Substrate

One of the questions to receive considerable attention here is the effect of the nature of the substrate on the fauna attaching to it. A number of sessile organisms show considerable substrate specificity, or sensitivity to differences in substrate, and are not commonly found on certain surfaces. Young (1941), in a general study of periphyton, observed that different substrates under identical conditions bear different kinds of periphyton. The chief difference is that organisms occur in varying proportions, although some species are completely absent from certain surfaces; Gloeotrichia lived abundantly on Scirpus, but not glass slides or ropes, although rope seemed more suitable for filamentous algae. Live Scirpus is smoother than dead, and has a hydrofuge surface which may explain the relative paucity of periphyton on live plants.

The characteristics of algae as substrates for diatoms received considerable attention from Cholnoky (1927). He studied the distribution of diatoms on filaments and Cladophora and Oedogonium, and found that parts of cells which were undergoing active growth by stretching of the cell wall carried few, if any epiphytes, since those that attached would soon fall off.

Keiser (1921) reported that species of fresh water crustacea with hydrophil surfaces (Copepods) car-

ried a large and more varied fauna of peritrichous Protozoa than those with hydrofuge surfaces (Cladocera). This simple, physical explanation does not seem to apply to substrate limitations recorded for other peritrichs recorded by Stiller (1940). He found two species of Vorticella which attached only to Gloeotrichia, another which attached only to Anabaena, and still another which attached only to the gelatinous matrix of colonies of the rotifer *Conochilus hippocrepis*.

Pelmatohydra evidently exhibits a certain amount of substrate selection. Miller (1936) indicated that plants overgrown with algal periphyton are not used extensively by Pelmatohydra, and Young (1941) showed an inverse numerical relationship between Gloeotrichia and Pelmatohydra. This effect may be simply the results of difficulty for such animals to attach to the loose, irregular mat of periphyton, but Young pointed out further that tree twigs, even when bare of algal periphyton, do not carry many Pelmatohydra.

Bryozoa also have some degree of substrate preference. Brown (1933) mentioned a distinct avoidance of Chara by all Bryozoa, evidently because of the odorous sulfur-containing compound secreted by the plant. In general, recumbent plants bear fewer Bryozoa than those which stand upright. Fredericella and Plumatella favor different substrates, the former evidently preferring rounded, or finely divided leaves, the latter preferring broad, flat leaves. Marine Byrozoa also have definite substrate requirements as shown by Hutchins (1941), who listed nine species which attached only to soft substrates such as algae and hydroid stems, and ten species attached only to shells, rocks, piles and other hard objects. There were eight species with less rigorous requirements which attached to both kinds of substrate.

The microscopic marine sessile organisms have received considerable attention because of their economically important role in fouling ships. Coe (1932) compared the attachment of organisms to wood and cement blocks immersed in the sea, and found that there was a great difference in the flora and fauna on the two surfaces. Coe & Allen (1937) studied further the attachment to glass plates, particularly with reference to the effect of the primary film of bacteria on attachment by larger organisms. Presence of bacteria facilitated the development of a periphyton. ZoBell (1936) has also discussed this point.

The larvae of some marine organisms avoid light colored surfaces and favor dark ones. Pomerat & Reiner (1942) showed that a greater number of barnacles attach to plates made of black glass, fewer to opal glass, and least of all to clear glass except at night, when equal numbers attach to all. The effect of the slope of the substrate was also studied. In general, most organisms attach to the under side of horizontal plates, least to the upper side, and intermediate numbers to sloping and vertical plates, as would be expected if the larvae were swimming up from a bed of reproducing individuals. Barnacles, however, showed a less regular response to the slope of substrate than did other organisms.

Krecker (1939) investigated the fauna of a number of freshwater plants growing together, and found considerable quantitative and qualitative differences in the animal populations of the various species when the amount of plant studied was measured on the basis of the length of stem. Some of the quantitative variation may be explained as a result of different areas of leaf associated with unit length of stem on account of morphological differences, but some clearly must depend on some other character of the plants. For instance, Myriophyllum carried the greatest number of individuals, but the fauna on Elodea was of the greatest taxonomic diversity.

An example of apparent substrate selection is the fauna on various forms of Sargassum in the Sargasso Sea, but there is evidence that faunal differences are a result of balance between the rates of extension of plants and animals (Burkenroad 1939).

That free-swimming animals may show considerable dependence on a solid substrate was demonstrated by Picken (1937). Many species of small ciliate Protozoa rarely swim freely in the water, but remain in contact with algal filaments. Thus a group of Protozoa may be bound together into a sort of community by a clump of blue-green algae, and complicated interactions between the animals and algae established. This often leads, after progressive development of the fauna, to destruction of the algae with consequent disbanding of the animals. Small, browsing rotifers (Lepadella, Colurella, some Lecane) evidently find the periphyton to be an important component of the habitat, providing as it does food and cover, in the same sense as in studies of game animals. Evidence can be found in the work of Meuche (1939). The relation between Nematodes and the diatom lasion has been discussed by Meschkat (1934). Here the animals not only live in the laminated diatom growth, but strongly affect the development of the periphyton during the year by keeping circular areas swept free of diatoms. In this way, a great number of relatively large spaces and tunnels are formed in the thick layer. These may well serve as shelter for organisms too large to fit into the finer structure of the unmodified lasion.

The Relation to Surface as Such

The general ecological significance of surfaces needs consideration. It is known that an increase in the ratio of surface area to volume of a vessel of water, as by reducing the size or adding glass wool, increases relative bacterial activity as measured by oxygen consumption. This is a result of the increased numbers of periphytic bacteria (ZoBell 1936, ZoBell & Anderson 1936), and undoubtedly alters the biological nature of the vessel when considered as a habitat for animals. Similarly, increase of the bounding surface of a lake by growth of large beds of vegetation alters the ecological nature of the lake by offering a large surface for attachment of periphytic organisms of all kinds; the productivity of a

lake is thus increased not only by the plants themselves, but also by the mere existence of solid surfaces. A numerical evaluation of the effect will be given subsequently.

Acknowledgments

During the course of the present work, the author has received a great deal of help for which he owes a heavy debt of gratitude. Professor G. Evelyn Hutchinson has, by his constant, stimulative suggestion and guidance, been of utmost importance to the conduct and completion of the work. Mr. F. J. Myers has been extremely generous in making available information, material and many opportunities for collecting in New Jersey and Pennsylvania. Dr. Chancey Juday furthered the work immeasurably by making it possible to collect in the Trout Lake Region of Wisconsin and to consult unpublished data. The Osborn Zoological Laboratory under the direction of Dr. L. L. Woodruff supplied considerable gasoline for collecting in Connecticut. Part of the work was done during tenure of the Annie G. K. Garland Scholarship. Dr. N. C. Fassett of the University of Wisconsin kindly examined specimens of aquatic plants and furnished identifications which are incorporated into the paper. Dr. Francis Drouet identified some blue-green algae. Dr. O. W. Young of Weber College, Utah, permitted the author to examine a copy of his Ph.D. dissertation on the periphyton of Douglas Lake, Michigan. Miss Anne Wollack kindly performed a number of chemical analyses. The author's wife has helped in many ways since the beginning of the work. Many other people with whom the author has been associated, too numerous to list individually, have helped in a variety of ways. To all of these people the author is glad to express his gratitude.

THE SESSILE ROTATORIA

Taxonomy and Life History

The sessile Rotatoria have been defined (Edmondson 1938, 1940) as consisting of all members of the families Flosculariidae and Conochilidae of the suborder Collothecacaea, using the classification of Remane (1929). The group is taxonomically diversified, and comparable to the Rhizota in Hudson's old classification (Hudson & Gosse 1886). Each of the families has some free-swimming species which live either singly or in colonies. In a narrower and more literal sense, sessile rotifers are those which live attached to a solid substrate for most of their lives, and it is to these that the present report is limited, including only truly sessile Flosculariidae and Collothecidae. A list is given here of the species encountered with indication of the number of times collected in each state. Abbreviations are C, Connecticut; W, Wisconsin; M, Massachusetts; P, Pennsylvania; NJ, New Jersey; NY, New York; NH, New Hampshire; V, Vermont.

COLLOTHECIDAE

Acyclus inquietus (Leidy) W 1, C 1.
Collotheca algicola (Hudson) W 9, C 7, M 1, P 1, NJ 1.
  var. *tenera* (Edmondson) NH 1.
  ambigua (Hudson) W 5, C 2.
  annulata (Hood) C 1.
  campanulata (Dobie) W 17, C 12, NH 3, NY 1, P 4, NJ 1.
  var. *longicaudata* (Hudson) W 6, C 2, P 1, NJ 1.
  coronetta (Cubitt) W 7, C 3, P 1.
  corynetis Edmondson W 7, P 2.
  cucculata (Hood) W 1.
  edentata (Collins) C 1, NJ 1.
  ferox (Penard) C 1, W 1(?).
  gracilipes Edmondson W 7, C 5, NH 1, NJ 1, P 1.
  heptabrachiata (Schoch) W 4, NJ 2.
  var. *diadema* W 13.
  judayi Edmondson W 2.
  ornata (Ehrenberg) W 14, C 9, P 2.
  var. *cornuta* (Dobie) W 26, C 20, M 1, NH 2, P 1, NJ 2.
  sessilis (Milne) W 1.
  stephanochaeta Edmondson W 2, C 1.
  trilobata (Collins) W 4, C 8, NH 2, P 1.
  sp. (see Edmondson, 1940) W 1.
Cupelopagis vorax (Leidy) W 7, C 12, P 3.
Stephanoceros fimbriatus (Goldfuss) W 17, C 10, M 1, NH 2, P 3, NJ 1.
  millsii (Kellicott) W 9, C 5, NH 2, P 1, NJ 1.

FLOSCULARIIDAE

Beauchampia crucigera (Dutrochet) W 8, C 15, M 1, NH 1, P 1, NJ 1.
Floscularia conifera (Hudson) W 17, C 19, M 1, NH 2, P 3, NJ 2.
  decora Edmondson W 6.
  janus (Hudson) W 18, C 11, NH 3, NY 1, P 4.
  melicerta (Ehrenberg) W 5, C 3.
  pedunculata (Joliet) W 4, P 6, NJ 2.
  ringens (Linnaeus) W 10, C 10, NH 3, P 12, NJ 1.
Lacinularia flosculosa (Müller) W 5, C 2, P 1.
Limnias ceratophylli Schrank W 12, C 7, NY 1, P 5.
  melicerta Weisse W 20, C 21, M 1, NH 2, NY 1, P 6, NJ 4.
  myriophylli (Tatem) NJ 1.
  shiawasseensis Kellicott C 1.
Octotrocha speciosa Thorpe W 11, C 2.
Pseudoecistes rotifer Stenroos W 3, C 1, P 3, NJ 2.
Ptygura barbata Edmondson W 4, C 4, M 1, V 1, NH 1, P 5.
  beauchampi Edmondson W 28, C 6, P 4, NJ 1.
  brevis (Rousselet) W 5, C 6, NH 1.
  cristata (Murray) W 1.
  crystallina (Ehrenberg) W 19, C 12, NH 2, P 2, NJ 1.
  linguata Edmondson W 5.
  longicornis (Davis) C 2, NJ 1.
  longicornis var. bispicata n.* W 25, C 15, M 1, NH 2, NY 1, P 8, NJ 2.
  longipes (Wills) W 2, C 1, P 2.

* *Ptygura longicornis* var. bispicata, n. This name will be used throughout to refer to a small *Ptygura* which differs from *P. longicornis* only in the possession of a pair of cuticular hooks on the dorsal side of the neck just posterior to the corona. This form is apparently undescribed, although it is very common. Kellicott (1888) apparently found this and thought it was the type form of *P. longicornis*. The present author for years has called the variety *P. brachiata* on account of the formal resemblance in certain ways to Hudson's description of that species, and has recorded it from Wisconsin under that name (1940). It is evident that the species really has nothing to do with *P. brachiata* which the author has never seen. *P. longicornis bispicata* will receive a more complete description in another publication.

melicerta Ehrenberg W 3, C 12, P 1.
var. *mucicola* (Kellicott) W 21, C 21, NH 1.
var. *socialis* (Weber) W 17, C 5, NY 1(?).
pectinifer (Murray) W 1.
pedunculata Edmondson W 10, C 5, NH 1, NJ 1.
pilula (Cubitt) W 30, C 11, M 1, NH 2, NY 1, P 5.
seminatans Edmondson W 1, NJ 2.
tacita Edmondson W 1, C 2.
velata (Gosse) W 6, P 1.
Sinantherina ariprepes Edmondson W 5, C 4, NH 1, P 1.
socialis (Linnaeus) W 7, C 6, NJ 3.

Most species live attached singly to aquatic plants, and secrete a tube into which the animal can retreat for protection. Eggs are laid in the tube where they remain until hatching. The young animal, usually called a larva although true metamorphosis can hardly be said to exist, swims freely until it encounters a suitable substrate to which it attaches. After a short period of rapid differential growth, the conical young animal assumes the shape of the adult. Once a larva attaches, it does not leave the substrate unless knocked off, in which case it cannot reattach. There are three exceptions: *Ptygura seminatans* and *Pseudoecistes rotifer* regularly leave the substrate when disturbed and swim freely. Certainly the former and probably the latter can reattach. Relatively young *Cupelopagis vorax*, if removed gently, can reattach, but probably do not leave the substrate voluntarily. Several important species are illustrated in Figure 1.

Materials and Methods

The material on which this study is based was collected mostly from ponds, bogs and the bays and shallow littoral of lakes. One hundred and ninety-four localities were sampled, some repeatedly. These were in Wisconsin, Connecticut, Pennsylvania, New Jersey, New York, Vermont, New Hampshire and Massachusetts. Plants were collected with the hands, or with a variety of simple equipment such as hooked poles, grapples and dredges. The plants were put into one or two quart jars without crowding. Rotifers are firmly attached, but rough handling should be avoided.

In the laboratory, finely divided leaves, such as those of Myriophyllum and Utricularia were examined entire or in parts in a Syracuse dish filled with pond water. Broad leaves were cut into strips and examined edgewise. In all manipulations, iridectomy scissors and watchmakers' forceps were most useful.

ASSOCIATION OF SPECIES

The number of species found in the localities varied from none to nineteen, and species occurred in various combinations. It is of interest to determine whether rotifers are distributed at random through a series of localities, or whether they are arranged in associations dependent on environmental or biological factors. Such associations of sponges and entomo-

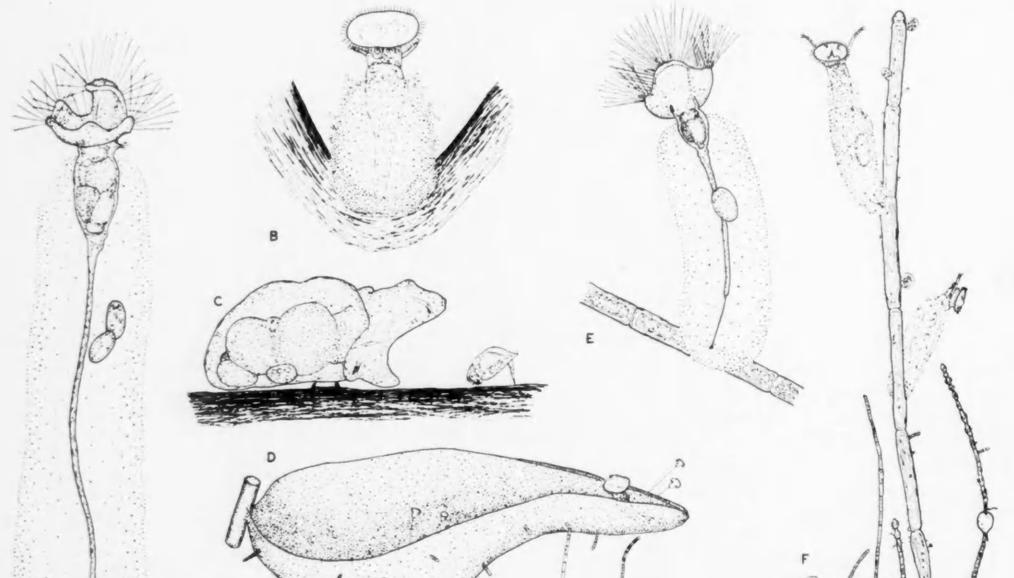

Fig. 1. Sessile Rotatoria. A, *Collotheca gracilipes* on *Utricularia vulgaris americana* with two eggs in the tube; B, *Ptygura brevis* in a fork of *Ceratophyllum demersum*; C, *Cupelopagis vorax* about to catch a *Colurella bicuspidata*; D, *Ptygura velata* in a leaf of *Sphagnum erythrocalyx*; E, *Collotheca campanulata* on *Oedogonium* sp.; F, *Ptygura barbata* on *Oedogonium* sp. which is attached to *Utricularia purpurea*.

straca in fresh water have been discussed to some extent by Jewell (1935) and Carl (1940) respectively.

Association of species can be studied by a method based on elementary probability theory. The method was suggested by Professor G. E. Hutchinson to the author who used it in an unfinished investigation of plankton Rotatoria, a preliminary report of which was made at the meeting of the Limnological Society of America at Indianapolis, Indiana, on December 29, 1937. If collections are made from a large enough number of lakes, the fraction of lakes in which a species occurs can be taken as the probability of finding that species in the same or a similar set of collections from the same lakes. Then if two species, A and B are found in a fraction p and a fraction q, respectively, of the total number of lakes examined, three situations are possible.

1. If the species are distributed at random and independently, they should occur together in a fraction pq of the total number of lakes.

2. If the species form an association, or are limited in the same way by environmental factors, they should occur together in some fraction of the lakes greater than pq.

3. If the species are mutually exclusive, or replace each other because of differences in tolerance to environmental factors, or for any other reason, they should occur together in some fraction of the lakes less than pq.

Given the number of lakes investigated and the number of lakes in which each species occurred, we can calculate the fraction of lakes inhabited by each species. By multiplying the fractions together in pairs we can find the fraction of lakes in which each pair should occur if distributed independently of each other at random, and translate this fraction into the actual number of lakes in which each pair should be found. The actual calculation, of course, can be simplified, and accomplished with two easy settings of a slide rule. When the calculated and observed values are compared, many differences will be found as the result of chance variation, but the significance of the differences can be tested by chi-square which is applicable to this situation (cf. Simpson & Roe 1939). When the expected number was as small as five or less, Yates' correction was made (Snedecor 1938). For present purposes, the 5% level of probability (chi-square of 3.8) was taken as indicating a significant difference between calculated and observed numbers. The 1% level of probability (chi-square of 6.6) represents a highly significant difference. This applies to all use of chi-square in this paper. Yates' correction tends to over-correct (E. B. Wilson 1941), so associations which remain significant after the correction is applied may be taken as really significant even though small numbers are involved.

Table 1 shows data for some of the more common sessile Rotatoria collected. Given are the number of times each species was collected, the number of times it was found with each of the others, and the number of times it was expected with each on the basis of random, independent distribution. Highly significant differences are shown by bold faced type (1% level), while less significant differences are shown in italics (5% level). For example, *Floscularia conifera* and *Collotheca campanulata* were observed to occur together 16 times, while the expected number is only 8; the difference is highly significant. On the other hand, *Floscularia conifera* and *Collotheca coronetta* occurred together 5 times rather than the predicted 2, but this difference is not significant according to criteria used.

Many significant associations exist. Often two species associated with a third are not associated with each other to a significant extent. This may be a result of reaction to more than one environmental factor. Note that of the 194 localities used for Table 1, 23 did not contain any sessile species. While continued examination would probably reveal the presence of rotifers, the localities must be regarded as rotiferless under the conditions in which the lists were compiled. If the calculations of expected association are based on the 171 lakes with rotifers, disregarding the others, the calculated number is made about 10% larger, and some associations are reduced to insignificance, although most are left unchanged. Yet to disregard a number of the lakes which are as much a part of the data as those with rotifers is illogical. For this reason, the full number of lakes was used in the calculations, but two levels of probability were differentiated.

Very few cases of apparent mutual exclusion were found. *Ptygura melicerta mucicola* and *Floscularia pedunculata* seem to replace each other, significant to 5%. Other species with which *P. m. mucicola* was found less frequently than expected were *Collotheca coronetta* and *Pseudoecistes rotifer*. These, and the other differences marked with an asterisk in Table 1 are not large enough to be significant, but they may be indicative. In general, out of 561 possible pairs, there are 71 associations significant to 1% and 57 significant to 5% but not 1%. There are no replacements significant to 1%, only one significant to 5%, though such a level of significance implies that with random distribution, about 28 pairs of apparent exclusion might have been expected. There were about 16 indications of possible replacement. The strong tendency towards association and away from exclusion or replacement may be taken as evidence that cases of strong interspecific competition are rare among the sessile Rotatoria. This is reasonable in view of the general abundance of their food and the usual rather low population densities encountered. Even when one species is found in very great abundance in a collection, there is apt to be a large number of other species present in smaller numbers. Inter- and intraspecific competition probably operate only under special circumstances which are too rare to have an effect on the general distribution of species. Moreover, many of the cases of possible exclusion, if valid, might be explained on the basis of chemical tolerance as will be seen. Hutchinson (1940) gave a discussion of the possible effect of changing environmental conditions on competitive

relationships among certain planktonic organisms, and showed that environmental control of competition very likely has an effect on the seasonal succession of some species.

Following are listed five groups of species. Each list is headed by a species which is associated with all others in the list at least to the 5% level of probability. Species marked with an asterisk are associated with the one at the head of the list to the 1% level or better. Such groups might be expected to have certain ecological properties in common, for limitations would tend to bring the species into the same habitats.

Beauchampia crucigera
Collotheca algicola
campanulata
*ornata**
*ornata cornuta**
*trilobata**
*Floscularia conifera**
*Limnias melicerta**
*Ptygura barbata**
*brevis**
*crystallina**
longicornis bispicata
melicerta mucicola

Collotheca gracilipes
ornata
ornata cornuta
trilobata
Floscularia conifera
Limnias melicerta

Collotheca campanulata
algicola
ornata
*ornata cornuta**
*trilobata**
*Cupelopagis vorax**
Beauchampia crucigera
*Floscularia conifera**
*janus**
*ringens**
Limnias ceratophylli
*Ptygura barbata**
*crystallina**
*longicornis bispicata**
*melicerta mucicola**

TABLE 1. Frequency of co-occurrence of pairs of species of sessile Rotatoria. The first figure in each cell of the table shows the number of localities in which the pair was observed to occur together. The second figure, in parentheses, shows the number of times the pair was expected to occur together on the basis of random, independent distribution as calculated by the method described in the text. The total number of localities in which each species occurred in the 194 investigated is shown in parentheses after the name of the species. Italics

	Collotheca campanulata	*c. longicaudata*	*coronetta*	*corynetis*	*gracilipes*	*heptabrachiata*	*h. diadema*	*ornata*	*o. cornuta*	*trilobata*	*Cupelopagis vorax*	*Stephanoceros fimbriatus*	*millsii*	*Beauchampia crucigera*	*Floscularia conifera*	*janus*
Collotheca algicola (19)	**9 (3)**	0 (1)	0 (1)	2 (1)	2 (1)	1 (1)	0 (1)	5 (2)	*9 (4)*	4 (2)	3 (2)	9 (3)	4 (2)	*6 (2)*	*9 (4)*	7 (4)
campanulata (36)		2 (2)	3 (2)	0 (2)	5 (3)	2 (1)	1 (2)	*9 (4)*	**20 (9)**	**10 (3)**	8 (3)	**13 (6)**	8 (3)	*9 (4)*	**16 (8)**	**18 (7)**
c. longicaudata (10)			2 (1)	3 (0)	0 (1)	1 (0)	2 (1)	3 (1)	*6 (2)*	3 (1)	1 (1)	1 (2)	1 (1)	3 (1)	4 (2)	1 (2)
coronetta (11)				1 (0)	1 (1)	2 (0)	*4 (1)*	7 (1)	*7 (3)*	*4 (1)*	*4 (1)*	2 (2)	1 (1)	2 (1)	5 (2)	4 (2)
corynetis (9)					0 (1)	1 (0)	2 (1)	3 (1)	3 (2)	2 (1)	0 (1)	1 (2)	2 (4)	0 (1)	4 (2)	2 (2)
gracilipes (15)						0 (0)	2 (1)	*6 (2)*	*9 (4)*	*4 (1)*	3 (1)	3 (3)	0 (1)	1 (2)	**11 (3)**	3 (3)
heptabrachiata (6)							0 (1)	2 (1)	1 (1)	0 (1)	0 (1)	0 (1)	0 (1)	0 (1)	0 (1)	0 (1)
h. diadema (13)								3 (2)	5 (3)	*5 (1)*	1 (1)	1 (2)	3 (1)	1 (1)	5 (3)	1 (2)
ornata (25)									**16 (6)**	9 (2)	7 (2)	7 (4)	7 (2)	8 (3)	10 (6)	6 (5)
o. cornuta (47)										**13 (4)**	**12 (4)**	*14 (8)*	**10 (4)**	**14 (5)**	**23 (11)**	10 (9)
trilobata (17)											*4 (1)*	*7 (3)*	7 (2)	8 (2)	**11 (4)**	**14 (3)**
Cupelopagis vorax (18)												6 (3)	1 (2)	4 (2)	8 (4)	4 (3)
Stephanoceros fimbriatus (33)													3 (3)	6 (4)	11 (7)	9 (6)
millsii (19)														5 (2)	7 (4)	3 (4)
Beauchampia crucigera (22)															**12 (5)**	6 (4)
Floscularia conifera (46)																9 (9)
janus (37)																
ringens (34)																
pedunculata (18)																
Limnias ceratophylli (23)																
melicerta (54)																
Octotrocha speciosa (13)																
Pseudoecistes rotifer (9)																
Ptygura barbata (15)																
beauchampi (39)																
brevis (11)																
crystallina (38)																
longicornis bispicata (51)																
melicerta (16)																
m. mucicola (42)																
m. socialis (22)																
pedunculata (16)																
pilula (49)																
Sinantherina ariprepes (9)																

Stephanoceros millsii
*Collotheca campanulata**
*ornata**
*ornata cornuta**
*trilobata**
*Ptygura barbata**
beauchampi
Ptygura melicerta mucicola
melicerta (type)*
*melicerta socialis**
*beauchampi**
*brevis**
crystallina
*longicornis bispicata**
*pedunculata**
Beauchampia crucigera
*Collotheca algicola**
*campanulata**
Floscularia conifera
pedunculata
Limnias melicerta
Sinantherina socialis
Stephanoceros fimbriatus

We turn now to a consideration of the effect of environmental factors on the distribution of rotifers in an attempt to discover the extent of such effect and the basis of the association of species.

FACTORS AFFECTING THE DISTRIBUTION OF SESSILE ROTATORIA

As a first method of attack, the lakes were arranged in order of concentration of the substance under consideration, and the series then divided into two equal groups, one of lakes above the median, the other of lakes below the median. In all discussion and tables to follow, the former is called the upper range, the latter the lower range. The number of occurrences of each species in each range was then counted from the faunal lists. Species indifferent to concentration of the substance should occur in equal numbers in the two ranges. Species which cannot tolerate high or low concentrations should occur in greater numbers on one side of the median than on the other. The significance of all differences found here were tested by chi-square as discussed before. This method of study has the advantage of easy calculation. It exposes immediately any marked trend for a species to occur at extremes of concen-

signify differences significant to the 5% level of probability or better (chi-square of 3.8 or larger) while bold-faced type indicates differences significant to the 1% level of probability or better (chi-square of 6.6 or larger). Yates' correction was used whenever one of the numbers was 5 or less. Cases of possible replacement are marked by an asterisk.

ringens	*pedunculata*	*Limnias ceratophylli*	*melicerta*	*Octotrocha speciosa*	*Pseudoecistes rotifer*	*Ptygura barbata*	*beauchampi*	*brevis*	*crystallina*	*longicornis bispicata*	*melicerta*	*m. mucicola*	*m. socialis*	*pedunculata*	*pilula*	*Sinantherina ariprepes*	*socialis*
3 (3)	0 (1)	3 (2)	_10 (5)_	2 (1)	0 (1)	5 (1)	**10 (4)**	**5 (1)**	5 (3)	7 (5)	3 (2)	**14 (4)**	3 (2)	5 (2)	5 (5)	3 (1)	3 (2)
15 (6)	1 (3)*	_9 (4)_	14 (10)	3 (2)	2 (2)	**9 (3)**	12 (7)	3 (2)	**15 (7)**	**18 (9)**	3 (3)	**17 (8)**	3 (4)	6 (3)	12 (9)	4 (2)	3 (3)
1 (2)	1 (1)	1 (1)	3 (3)	0 (1)	1 (1)	2 (1)	4 (2)	0 (1)	2 (2)	6 (3)	1 (1)	1 (2)	0 (1)	0 (1)	**7 (2)**	0 (1)	0 (1)
1 (2)	2 (1)	0 (1)	4 (3)	3 (1)	1 (1)	1 (1)	5 (2)	2 (1)	4 (2)	**9 (3)**	0 (1)	4 (2)	1 (1)	3 (1)	_7 (3)_	1 (1)	0 (1)
0 (2)*	1 (1)	0 (1)	3 (3)	2 (1)	1 (0)	2 (1)	4 (2)	0 (1)	1 (2)	4 (2)	0 (1)	0 (2)*	0 (1)	1 (1)	6 (2)	0 (0)	0 (1)
5 (3)	0 (1)	2 (2)	_9 (4)_	2 (1)	0 (1)	1 (1)	5 (3)	1 (1)	4 (3)	5 (4)	2 (1)	5 (3)	1 (2)	3 (1)	4 (4)	3 (2)	1 (1)
1 (1)	0 (1)	0 (1)	0 (2)	0 (0)	0 (0)	0 (1)	0 (1)	1 (0)	0 (1)	0 (2)	0 (1)	0 (1)	1 (1)	0 (1)	2 (1)	0 (0)	0 (1)
0 (2)*	2 (1)	0 (2)	1 (3)	4 (1)	1 (1)	1 (1)	5 (3)	0 (1)	2 (2)	**9 (3)**	0 (1)	0 (3)	0 (1)	0 (1)	_7 (3)_	0 (1)	1 (1)
8 (4)	2 (2)	4 (3)	_13 (7)_	5 (2)	2 (1)	**7 (2)**	9 (5)	3 (2)	8 (5)	**14 (6)**	2 (2)	7 (5)	2 (3)	4 (2)	**16 (6)**	2 (1)	2 (2)
17 (8)	2 (4)	7 (5)	**24 (13)**	5 (3)	2 (2)	7 (4)	_15 (9)_	5 (3)	**19 (9)**	**24 (12)**	3 (4)	14 (10)	3 (5)*	6 (4)	28 (12)	1 (2)	4 (4)
5 (3)	2 (2)	3 (2)	_10 (5)_	1 (1)	0 (1)	_6 (1)_	4 (3)	_4 (1)_	9 (3)	**13 (4)**	2 (1)	7 (3)	1 (2)	3 (1)	8 (4)	2 (1)	0 (1)
_9 (3)_	1 (2)	_6 (2)_	_9 (5)_	1 (1)	2 (1)	3 (1)	6 (4)	_4 (1)_	**10 (3)**	9 (5)	3 (1)	7 (4)	2 (2)	3 (1)	4 (4)	2 (1)	**5 (1)**
10 (6)	0 (3)*	7 (4)	10 (9)	2 (2)	0 (2)*	5 (3)	9 (6)	_6 (2)_	11 (6)	13 (8)	4 (3)	_13 (7)_	_7 (3)_	5 (3)	13 (8)	4 (2)	5 (3)
4 (3)	1 (2)	2 (2)	6 (5)	1 (1)	1 (1)	**5 (1)**	_1 (4)_*	1 (1)	4 (3)	3 (5)	2 (2)	4 (4)	0 (2)*	1 (2)	7 (5)	2 (1)	0 (2)
8 (4)	1 (2)	4 (3)	**13 (6)**	2 (1)	2 (1)	**6 (1)**	6 (4)	**5 (1)**	**11 (4)**	_12 (6)_	5 (2)	_11 (5)_	3 (2)	4 (2)	6 (5)	2 (1)	1 (2)
10 (8)	2 (4)	7 (5)	**27 (13)**	4 (3)	3 (2)	9 (3)	14 (9)	4 (3)	**17 (9)**	**21 (12)**	6 (4)	_17 (10)_	4 (5)	_9 (4)_	**21 (11)**	_6 (2)_	2 (4)
13 (6)	2 (3)	5 (4)	11 (9)	2 (2)	4 (2)	5 (3)	9 (7)	3 (2)	_13 (7)_	13 (9)	5 (3)	13 (8)	6 (4)	4 (3)	7 (9)	3 (2)	4 (3)
	4 (3)	4 (4)	**18 (9)**	4 (2)	5 (2)	4 (3)	5 (7)	4 (2)	_12 (6)_	**18 (9)**	3 (3)	5 (7)	_1 (4)_*	1 (3)	11 (8)	3 (2)	2 (3)
		0 (2)	4 (5)	0 (1)	3 (1)	1 (1)	_1 (4)_*	0 (1)	5 (3)	5 (5)	1 (1)	_0 (4)_*	1 (2)	0 (1)	2 (4)	1 (1)	0 (1)
			6 (6)	0 (2)*	2 (1)	2 (1)	8 (5)	0 (1)	6 (4)	5 (6)	3 (2)	6 (5)	2 (3)	3 (2)	5 (6)	1 (0)	3 (2)
				5 (4)	5 (2)	8 (4)	12 (10)	8 (3)	_17 (10)_	_22 (13)_	8 (4)	_19 (11)_	6 (4)	8 (4)	18 (13)	**7 (2)**	6 (4)
					2 (1)	4 (1)	4 (2)	0 (1)	4 (2)	6 (3)	1 (1)	1 (3)	1 (1)	1 (1)	**11 (3)**	1 (1)	2 (1)
						3 (1)	2 (2)	0 (0)	2 (2)	3 (2)	0 (1)	0 (2)*	0 (1)	0 (1)	3 (2)	0 (0)	0 (1)
							2 (3)	1 (1)	4 (3)	6 (4)	0 (1)	4 (3)	0 (2)*	1 (1)	6 (4)	1 (1)	0 (1)
								_6)2)_	6 (7)	_18 (10)_	3 (3)	**17 (8)**	8 (4)	_7 (3)_	11 (10)	3 (2)	5 (3)
									6 (1)	6 (3)	3 (1)	**9 (2)**	**5 (1)**	3 (1)	4 (3)	2 (1)	3 (1)
										6 (1)	9 (3)	_15 (8)_	6 (4)	3 (3)	_16 (9)_	4 (2)	5 (3)
											4 (3)	9 (3)	3 (6)*	_7 (3)_	**24 (13)**	3 (2)	2 (3)
												12 (3)	3 (2)	2 (1)	3 (4)	_4 (1)_	_4 (1)_
													12 (5)	9 (3)	8 (11)*	5 (2)	_7 (3)_
														3 (2)	4 (5)	3 (1)	2 (2)
															3 (4)	3 (1)	3 (1)
																1 (2)	3 (4)
																	1 (1)

tration, but gives no information about the extent of tolerance within each range. It may miss some significant responses to chemical concentration, particularly limitation to a narrow range centered on the median, but is unlikely to present spurious correlations if there is a reasonable number of lakes in each group. This method was supplemented by dividing the range of concentration into divisions of equal length, and studying the frequency of species in the various classes of concentration. Since this is based on units of concentration, it is necessary to take account of the number of lakes in each class of concentration. These methods, together with a tabulation of the extremes of concentration in which the species occurred should give an adequate idea of the distribution. If desired, of course, the group of collections can be studied further by quartiles, or even finer divisions, but for the present purposes, the median seemed sufficient. The foregoing list gives the largest and smallest values of pH and bicarbonate concentration, in that order, in which the species have been found.

Acyclus inquietus	7.0–8.8	38.4– 40.3
Collotheca algicola	6.2–8.8	10.4– 57.2
ambigua	5.5–8.5	9.2– 63.4
annulata	7.2	42.7
campanulata	5.2–8.8	18.3–165.3
c. longicaudata	4.6–6.9	48.8– 9.2
coronetta	4.6–7.6	3.0– 59.2
corynetis	4.1–7.5	4.9– 16.5
cucculata	5.6	....
edentata	7.3	63.4
ferox	8.5	....
gracilipes	6.0–8.5	1.8–317.8
heptabrachiata	3.5–5.6	3.0
h. diadema	4.5–7.5	3.0– 16.5
judayi	5.7–7.4	9.2– 16.5
ornata	3.5–8.4	3.0–131.2
o. cornuta	4.6–8.7	1.8–206.8
sessilis	ca. 4.0	....
stephanochaeta	5.7–7.4	9.2– 28.7
trilobata	4.1–7.9	3.7– 58.9
Cupelopagis vorax	5.2–8.5	3.7–265.4
Stephanoceros fimbriatus	5.7–8.8	3.7–265.4
millsii	5.2–7.4	3.7–141.5
Beauchampia crucigera	5.8–7.6	1.8– 59.2
Floscularia conifera	4.6–7.9	1.8–317.8
decora	5.0–7.0	3.6– 7.2
janus	5.2–9.2	1.8–199.5
melicerta	4.6–7.6	9.2– 58.9
pedunculata	4.1–6.8	6.1–141.5
ringens	4.8–8.9	1.8–317.8
Lacinularia flosculosa	7.1–8.5	40.2–317.8
Limnias ceratophylli	6.0–8.8	7.3–265.4
melicerta	4.1–8.9	1.8–317.8
myriophylli	7.2	....
shiawasseensis	6.9–7.6	21.4– 38.4
Octotrocha speciosa	5.7–7.5 (9.2?)	4.9– 32.9
Pseudoecistes rotifer	4.6–7.0	4.9–141.5
Ptygura barbata	5.2–7.1	5.5– 28.7
beauchampi	4.6–8.4	5.5–206.8
brevis	5.6–8.4	11.0–131.3
cristata	6.8	21.4
crystallina	4.6–8.2	1.8–317.8
linguata	5.2–6.9	3.6– 27.8
longicornis bispicata	4.1–8.8	1.8–165.3
longipes	6.4	....
melicerta	5.8–8.8	4.3– 63.4
m. mucicola	6.2–8.8	10.4–165.3
m. socialis	5.6–9.2	3.0– 92.7
pectinifer	7.2	42.7
pedunculata	5.0–9.2	11.9– 67.7
pilula	3.5–8.2	1.8–265.4
seminatans	5.7	9.2
tacita	5.7	9.2– 28.7
velata	4.0–8.4	3.0–131.2
Sinantherina ariprepes	5.9–7.9	5.5–317.8
socialis	5.9–9.2	3.0–265.4
Sphagnum	3.5–7.6	1.8– 61.3
Utricularia	4.1–8.9	1.8–317.8
Gloeotrichia	5.6–8.8	3.0–165.3
Collections	3.5–9.2	1.8–317.8

Hydrogen Ion

Active concentration of hydrogen ion is the factor which has received most attention in regard to the distribution of Rotatoria, and is the one for which most data are available in this study. Values of pH were determined as soon after collecting as possible, either colorimetrically or, more usually, potentiometrically. Data were obtained for 136 lakes. The range was 3.5-9.2, the median 6.8.

The list given previously shows the extreme values of pH in which species were found, while Table 2 gives the distribution of some species around the median value of pH. All species which showed a significant limitation to one side of the median are listed as well as some that did not. Chi-square values are given. The lists which follow show species which seem to react to pH in a definite way.

TABLE 2. Distribution of sessile Rotatoria around the median of pH. The number of occurrences above and below the median and the chi-square values are given. The number of lakes in each group is shown.

	Number of Occurrences in		Chi Square
	Lower Range (3.5–6.8)	Upper Range (6.9–9.2)	
Lakes			
New England	9	23	
Wisconsin	47	40	
Other	12	5	
Species			
Ptygura melicerta mucicola	5	34	21.4
Collotheca algicola	2	16	10.8
Sinantherina socialis	1	12	9.2
Collotheca heptabrachiata diadema	11	2	6.2
Stephanoceros fimbriatus	8	21	5.8
Ptygura pilula	28	13	5.4
Ptygura brevis	2	10	5.3
Ptygura melicerta socialis	6	16	4.5
Lacinularia flosculosa	0	6	4.2
Floscularia pedunculata	8	1	4.0
Ptygura beauchampi	13	24	3.2
Collotheca campanulata longicaudata	7	1	*2.1
Collotheca corynetis	7	1	*2.1
Collotheca campanulata	11	20	2.6
Stephanoceros millsii	10	4	2.5
Floscularia decora	5	1	1.5
Ptygura melicerta type	5	9	1.1
Cupelopagis vorax	5	11	2.2
Collotheca ornata cornuta	17	22	0.6
Limnias melicerta	20	26	0.8
Ptygura longicornis bispicata	25	21	0.3

*Without Yates' correction, these give significant chi square values.

Species occurring in lowest range (3.4-3.5, one locality):

Collotheca heptabrachiata
ornata
Ptygura pilula

Species occurring in the highest range (9.0-9.1, one locality):

Collotheca algicola
campanulata
Floscularia janus
Ptygura melicerta socialis
peduculata
Sinantherina socialis

Species living entirely below pH 7.0:

Collotheca campanulata longicaudata (found in 8 localities)
Floscularia decora (found in 5 localities)

Species able to live at pH 8.0 or greater (12 localities represented):

Acyclus inquietus
Collotheca algicola
ambigua
campanulata
gracilipes
*ornata**
*ornata cornuta**
Cupelopagis vorax
Stephanoceros fimbriatus
Floscularia janus
*ringens**
Lacinularia flosculosa
*Limnias melicerta**
ceratophylli
Octotrocha speciosa (?)
*Ptygura beauchampi**
*longicornis bispicata**
brevis
*crystallina**
melicerta
melicerta mucicola
melicerta socialis
*pedunculata**
*pilula**
*velata**
Sinantherina socialis

Ptygura pilula is interesting in that it definitely favors acid water, although it occurs through a very wide range of concentration (4.7 units). The other two species which have about as great a range, *Collotheca ornata* and *Limnias melicerta* have no preference for one part of the range. *Beauchampia crucigera* has the narrowest range of all, 1.8 units (found in 12 lakes), while *Ptygura barbata* in 9 lakes had a range almost as small (1.9).

BICARBONATE

The bicarbonate content of New England and Pennsylvania lakes was determined by titrating 100 cc. samples with 0.01 N. sulfuric acid, using the methyl orange end point. The number of cc. of acid used multiplied by a factor of 6.1 gives the milligrams per liter of bicarbonate ion, and this is the method of expression used here. The Wisconsin data were expressed as "bound carbon-dioxide" (Juday, Birge and Meloche 1935) which is five times the number of N/44 acid used in titrating 100 cc. of water. The Wisconsin figures were converted to bicarbonate by multiplying them by a factor of 2.8 $(= \frac{1}{5} \times \frac{100}{44} \times 6.1)$. Data are available from 96 lakes. The range is 1.8-317.8 and the median 28.1 mgm./1. Most Wisconsin determinations are from the records of the Trout Lake Limnological Laboratory.

* Species also found at pH of 5.0 or less.

Table 3 gives the distribution of some species around the median of bicarbonate, and the extreme values at which each was found were listed previously. Certain species had definite limitations with reference to bicarbonate as shown by the lists which follow.

TABLE 3. Distribution of sessile Rotatoria around the median of bicarbonate concentration. Explanation as in Table 2.

	Number of Occurrences in		Chi Square
	Lower Range (1.8-27.5 mgm./l.)	Upper Range (28.7-317.8 mgm./l.)	
LAKES			
New England	17	18	
Wisconsin	26	26	
Other	5	4	
SPECIES			
Ptygura melicerta mucicola	9	29	10.4
Ptygura brevis	1	10	7.3
Ptygura barbata	9	0	7.1
Ptygura pilula	19	6	6.7
Beauchampia crucigera	13	3	6.2
Collotheca corynetis	7	0	5.2
Stephanoceros millsii	10	2	5.2
Ptygura longicornis bispicata	21	9	4.8
Collotheca ornata	13	4	4.7
Octotrocha speciosa	8	1	4.0
Ptygura melicerta socialis	6	13	2.6
Ptygura pedunculata	3	9	3.0
Ptygura melicerta type	7	7	0.0
Collotheca heptabrachiata diadema	5	0	3.2
Lacinularia flosculosa	0	5	3.2
Collotheca algicola	5	11	2.2
Cupelopagis vorax	7	6	0.0
Collotheca ornata cornuta	16	12	0.6

Species found in a very wide range:

Collotheca gracilipes
Cupelopagis vorax
Stephanoceros fimbriatus
Floscularia conifera
Lacinularia flosculosa
Ptygura pilula
Sinantherina ariprepes

Species able to live in concentrations greater than 84 mgm./1.:

Collotheca campanulata
gracilipes
ornata
cornuta

Cupelopagis vorax
Floscularia conifera
janus
pedunculata
ringens
Lacinularia flosculosa
Limnias ceratophylli
melicerta
Pseudoecistes rotifer
Ptygura beauchampi
brevis
crystallina
longicornis bispicata
melicerta mucicola
melicerta socialis
pilula
velata
Sinantherina ariprepes
socialis
Stephanoceros fimbriatus
millsii

Species found in concentrations above 252 mgm./1.:

Collotheca gracilipes
Floscularia conifera
ringens
Limnias melicerta
Ptygura crystallina
Sinantherina ariprepes

Species found only in concentrations less than 84 mgm./1.:

Collotheca algicola
campanulata longicaudata
coronetta
corynetis
heptabrachiata diadema
judayi
stephanochaeta
trilobata
Beauchampia crucigera
Floscularia decora
melicerta
Octotrocha speciosa
Ptygura barbata
linguata
longipes
melicerta

Lacinularia flosculosa, which occurred too infrequently to give a significant chi-square, seems confined to the upper range of bicarbonate (as well as of pH). The type form of *Ptygura melicerta* is evenly distributed between the two ranges, although hard water is mildly favored by variety *socialis,* strongly favored by variety *mucicola.*

Calcium

Unfortunately, calcium determinations are available for only fifty of the lakes studied. Just one species gives a significant chi-square as shown by Table 4. Nevertheless, recalling the close correlation between calcium, bicarbonate and pH, demonstrated for Wisconsin by Juday, Birge & Meloche (1935), it may be suspected that the large number of small, unnamed, acid localities excluded from this discussion actually had a low calcium content, and a correlation with the rotifer fauna could be demonstrated, given a large enough number of determinations. A number of species occurred at concentrations as high as 38 mgm./1. and also at 5 mgm./1. or lower; they are listed.

Table 4. Distribution of sessile Rotatoria around the median of calcium. Explanation as in Table 2.

	Number of Occurrences in		Chi Square
	Lower Range (0.22-5.6 mgm./l.)	Upper Range (6.65-35.0 mgm./l.)	
Lakes			
Wisconsin	19	22	
Pennsylvania	6	3	
Species			
Ptygura melicerta mucicola	4	13	4.6
Collotheca corynetis	4	0	2.2
Stephanoceros millsii	4	0	2.2
Lacinularia flosculosa	0	4	2.2
Floscularia conifera	8	3	1.4
Ptygura pilula	8	3	1.4

Collotheca gracilipes
Floscularia conifera
ringens
Lacinularia flosculosa
Limnias melicerta
Ptygura pilula
Sinantherina socialis
Stephanoceros fimbriatus

Magnesium

Data on magnesium are available for 38 lakes in which rotifers were collected. The range was 0.088-23.5, median 2.8 mgm./1. The only species limited significantly is *Ptygura melicerta mucicola* which was found three times below the median, eleven times above. Species which tolerated concentrations of magnesium of at least 20 mgm./1. are listed here. All occurred at much lower concentrations as well.

Collotheca campanulata
gracilipes
ornata
ornata cornuta
Floscularia conifera
janus
Lacinularia flosculosa
Limnias melicerta
Ptygura longicornis bispicata
crystallina
velata
Sinantherina ariprepes

Conductivity

The conductivity of water, expressed as reciprocal megohms, inverse of resistance, is known for 50 of the lakes in which rotifers were collected. Conductivity is a measure of ionically dissociated material in the water, modified by the presence of large colloidal micelles. Conductivity then increases with mineralization of the water while added humus decreases it. since ions are adsorbed on the humus. There is, how-

ever, a general correlation between conductivity and certain dissolved solids, as demonstrated for Wisconsin by Juday & Birge (1933). The range studied was 6-245 reciprocal megohms with a median of 44. As a result of the small number of data, only *Ptygura melicerta mucicola* showed a significant limitation. Table 5 shows the distribution of several species. A

TABLE 5. Distribution of sessile Rotatoria around the median of conductivity. Explanation as in Table 2.

	Number of Occurrences in		Chi Square
	Lower Range (6-42)	Upper Range (45-245)	
Lakes			
Wisconsin	21	20	
Pennsylvania	4	5	
Species			
Ptygura melicerta mucicola	3	12	4.2
Octotrocha speciosa	5	0	3.2
Ptygura longicornis bispicata	10	5	1.2
Ptygura pilula	9	2	3.2
Collotheca ornata cornuta	7	1	3.1
Floscularia janus	13	5	3.4

number of species tended to occur in waters of low conductivity. These were

Collotheca corynetis
ornata
ornata cornuta
Ptygura longicornis bispicata
crystallina
pilula
Stephanoceros millsii

Other species occurred more frequently in waters of high conductivity. These were

Collotheca algicola
Lacinularia flosculosa
Ptygura melicerta socialis

Other Factors

Distribution of sessile rotifers seemed to show no correlation with dry weight of plankton, but there was evidence of a correlation with the color of the water; this might be expected since highly acid waters are usually deeply colored. Residue, expressed as milligrams per liter, is the material left after evaporation and ignition of a water sample, and might be expected to show the same general correlations as conductivity, at least in waters of low humus content. Only thirty-eight lakes were available, and just two significant limitations are exposed as shown in Table 6.

Little can be said about the effect of available food on distribution as no consistent observations of associated food organisms. The two families studied feed by radically different methods, and eat rather different food organisms. It may be expected that conditions which favor the existence of small ciliates such as Coleps and Colpoda will also favor many Collothecidae, while conditions favoring small flagellated algae, minute blue green algae and bacteria will also favor Flosculariidae. The work of Noland (1925) and Picken (1937) suggests that physical or biological factors can favor one or the other of these two sets of food organisms, and so likely affect the fauna.

TABLE 6. Distribution of sessile Rotatoria around the median of residue. Explanation as in Table 2.

	Number of Occurrences in		Chi Square
	Lower Range (14.9-47.5 mgm./l.)	Upper Range (49.3-98.6 mgm./l.)	
Lakes			
Wisconsin	19	19	
Species			
Ptygura melicerta mucicola	1	13	10.2
Ptygura melicerta socialis	2	10	5.2
Ptygura pilula	7	1	3.0
Beauchampia crucigera	4	0	2.2

In passing it may be noted that many of the limitations observed by their effects of the frequency with which species are found in a great number of collections are substantiated by data on the abundance of the same species in collections. For instance, *Ptygura pilula* has been found in extreme abundance in six localities, all of them quite acid (pH 3.5-6.1), despite the fact that the species can live in relatively hard, alkaline water.

Discussion

The data given seem to indicate a relationship between occurrence of certain species and the chemistry of the water. It is a fact of observation, for instance, that in 138 lakes, *Ptygura melicerta mucicola* tended to occur in the higher range of pH. The probability that the data given for the variety in Table 2 could be duplicated if there really were no relationship is considerably less than one in a hundred. This, as pointed out previously, does not necessarily mean that hydrogen ion is the factor to which the rotifer responds. The effective factor could be something which is correlated with pH, such as calcium or bicarbonate. This is exactly the situation exposed by Jewell's experiments with sponges (1939). Such experiments would be very difficult to perform with animals as small as rotifers, although culture experiments offer some hope for future work. Up to the present, the author has been unable to obtain lasting cultures in the laboratory. Another method of attacking the problem is to analyze field data. The correlation between environmental factors is not perfect, of course, so that in a large series of collections, it will usually be found that several with the same pH value will vary in bicarbonate concentration, and extreme collections may give information about the effective factor. Data of this sort provided by Yoshimura (1933) suggest that the cladoceran

Holopedium is calcifuge rather than acidophil. Table 7 summarizes the correlations with pH and bicarbonate of all species which are significantly limited by one or both.

TABLE 7. Species which are significantly limited with reference to the median of pH, bicarbonate concentration, or both, with the observed ranges of tolerance extracted from Table 4. U marks the species which are found most often in the upper range (above the median), L those which are found most often in the lower range (below the median).

Species	pH Range	Bicarbonate Range
Species which are limited with reference to pH, not bicarbonate.		
Collotheca algicola	U 6.2 - 8.8	10.4 - 57.2
h. diadema	L 4.5 - 7.5	3.0 - 16.5
Cupelopagis vorax	U 5.2 - 8.5	3.7 - 265.4
Floscularia pedunculata	L 4.1 - 6.8	6.6 - 141.5
Lacinularia flosculosa	U 7.1 - 8.5	40.2 - 317.8
Ptygura melicerta socialis	U 5.6 - 9.2	3.0 - 92.7
Sinantherina socialis	U 5.9 - 9.2	3.0 - 265.4
Stephanoceros fimbriatus	U 5.7 - 8.8	3.7 - 265.4
Species which are limited with reference to bicarbonate, not pH.		
Beauchampia crucigera	L 5.8 - 7.6	1.8 - 59.2
Collotheca corynetis	L 4.1 - 7.5	4.9 - 16.5
ornata	L 3.5 - 8.4	3.0 - 131.2
Octotrocha speciosa	L 5.7 - 7.5	4.9 - 32.9
Ptygura barbata	L 5.2 - 7.1	5.5 - 28.7
longicornis bispicata	L 4.1 - 8.8	1.8 - 165.3
Species which are limited with reference to both pH and bicarbonate.		
Ptygura melicerta mucicola	U 6.2 - 8.8	10.4 - 165.3
brevis	U 5.6 - 8.4	11.0 - 131.2
pilula	L 3.5 - 8.2	1.8 - 265.4

Beauchampia crucigera occurs in a narrow range of pH centered around neutrality. The bicarbonate range is rather narrow also. Figure 2 shows that the species had ample opportunity to occur at much higher and lower pH values and higher bicarbonate concentrations. It is unlikely that this is a random pattern especially when the strong association with *Ptygura longicornis bispicata,* also shown in the figure, is recalled. Very likely *Beauchampia crucigera* shows sensitivity to both pH and bicarbonate, being restricted by high and low values of the former, high values of the latter. *Ptygura barbata* may be limited the same way.

Collotheca heptabrachiata diadema occurred in waters as alkaline as pH 7.4, although the highest bicarbonate concentration in which it occurred was only 16.5 mgm./1. Probably this species is kept out of hard waters by alkaline earth bicarbonates rather than by the concomitant high pH. The distribution of *C. corynetis* is very similar, and is shown in Figure 2. It did not occur at all above the median concentration of bicarbonate.

The difficulty with determining the identity of effective environmental factors by this method is that the probabiltiy of finding any given species is so low that its absence from any class of lakes is not significant unless that class is represented by a great number of collections. The four species named above may be taken, however, as being almost certainly limited by the factors named. In addition, the varieties of *Ptygura melicerta* and *Collotheca algicola* are certainly limited by bicarbonate, but since they also show a very special selection of substrate, further discussion is postponed.

The data presented so far might be taken as evidence that the distribution of sessile rotifers is governed by chemical factors. But one of the most obvious and tangible parts of the habitat of sessile organisms has not yet been considered; the substrate. If substrate plants are limited in distribution by chemical factors, and if any sessile species is more or less limited to certain substrates, then, with the evidence already presented, it is impossible to know whether the primary requirement of many rotifers is a proper chemical environment or a proper substrate. This problem has received considerable attention.

THE RELATIONSHIP BETWEEN SESSILE ROTATORIA AND THEIR SUBSTRATE

THE EFFECT OF SURFACE AS SUCH

Shelford's statement, quoted by Frohne (1938), that the plants of a lake could be replaced by glass structures of the same shape, size and surface texture without greatly affecting the immediate food relationships, has been shown by Frohne to be rather overdrawn, but it is nevertheless true that *surface* as such plays an important part in aquatic ecology. One effect of the presence of surfaces can be demonstrated by calculating the maximal population of rotifers in a series of habitats differentiated largely by the amount of surface present. The three types chosen are: (1) pelagic region of lakes, with an inconsiderable amount of solid surface, (2) littoral region with considerable plant surface, and (3) capillary water of damp sand beaches with an enormous amount of surface. Data for maximal populations in each type of habitat are listed:

1. A casual search of literature on American plankton shows that the largest population of all free-swimming species to be expected is in the order of 1,200 rotifers per liter (e.g., Campbell 1941).

2. Ahlstrom (1933) made an extensive quantitative study of the free-swimming littoral fauna by dipping measured quantities of water from a small, weedy pond-like embayment of Lake Erie. The maximum population was 4,619 rotifers of all species per liter. Kofoid (1908) found a maximum of 5,200 in the net plankton of the Illinois River which contains many littoral species. Since one would expect to find larger numbers in immediate contact with the plant, data taken during the present studies are added. These will be given in detail in Part II at a later date. The maximum population of any sessile species ever treated quantitatively was about 25,000 individuals per liter on *Utricularia.* The volume calculated was that of a cylinder enclosed by the tips of the leaves. This number of rotifers does not include any free-swimming species, which are the only ones in the other determinations.

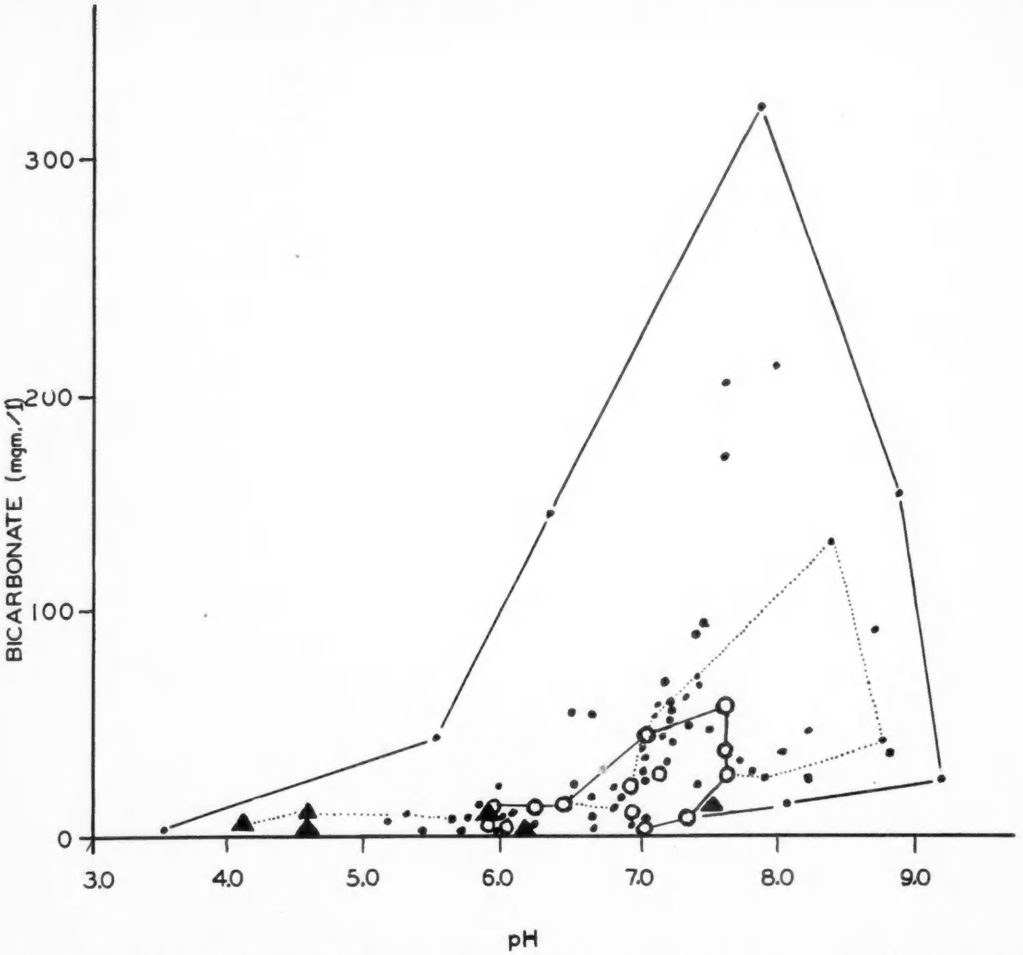

FIG. 2. Distribution of *Beauchampia crucigera* with r eference to pH and bicarbonate concentration (mgm./l.). Each dot represents observed values for a locality. Localities in which Beauchampia occurred are indicated by open circles, and the area in which they lie is outlined by a solid line. The outermost solid line enclosed the area in which all localities fall. For comparison, the area containing the points of occurrence of *Ptygura longicornis bispicata* is outlined by a finely dotted line, and the lakes containing *Collotheca corynetis* are represented by triangles.

3. Pennak's data (1940) on the sand fauna show that the maximum population of all rotifer species was in the order of 1,155,000 individuals per liter of damp sand, or about 4,620,000 per liter of the water contained therein, since a typical sand sample contained 25% water by volume.

These figures can be rounded and compared as follows:

Plankton	1,000	per liter
Littoral	5,000	
Sessile	25,000	
Sand	1,155,000	

While the ratio of surface to volume cannot be described quantitatively in a comparable manner, it is plain that the more surface there is, the larger the population which can develop, even if the surface is, in effect, made of glass.

FACTORS WHICH AFFECT THE DISTRIBUTION OF SUBSTRATE PLANTS

During the progress of this study, it became clear that different plants did not bear the same rotifer fauna, quantitatively or qualitatively. *Utricularia vulgaris americana* could usually be counted on to furnish more specimens of more species than any other plant in the same locality. There were some notable exceptions to this. Since some rotifers were apparently limited by chemical conditions, it was necessary to study factors affecting the distribution of plants to see if the fauna of different plants was different because both plants and animals were lim-

ited to the same habitats, or whether there was some quality about the plants themselves which made them suitable or unsuitable as substrate.

The data from Wisconsin and New England are treated separately here since collections in the two regions were made with different objectives. The Wisconsin collections were made to furnish lists of rotifers from as many different types of localities as possible and to furnish as much taxonomic material as possible. Most collections were made in the vicinity of the Trout Lake Limnological Laboratory in Vilas County, although some were made near Madison. The Trout Lake Region has been described by Juday and Birge (1930). Critical taxonomic studies of the flora were not made, but plants were usually identified to genus. For a study of distribution, it is convenient to divide them into three very arbitrary categories:

All species of Sphagnum.

All species of Utricularia (mostly *U. vulgaris americana*).

All other plants (chiefly Myriophyllum, Potamogeton, Megalodonta, Fontinalis, Anarcharis).

The distribution of each group was studied with reference to the median and range of each factor, in just the same as the distribution of rotifers. All three groups showed significant limitation by pH and bicarbonate, the first two groups being more common in soft, acid water, the third being more common in hard, alkaline water. The data are summarized in Table 8. There was some correlation with calcium, magnesium, and residue also. It may be surprising that such a heterogeneous group as the third should not extend further into the acid range, but the results are in general agreement with Fassett's findings in the same region (1930). Since most of the plants collected in Wisconsin were submersed forms with flexuous leaves and stems, the third group is almost equivalent to Fassett's Growth Form 1. Rossbach (1939) discussed the distribution of Utricularia. *U. vulgaris americana* is euryionic. Its tendency to occur in acid water in the Wisconsin collections is a result of the distribution of the collections. The species occurs in small, quiet localities, most of which were acid in these collections.

In New England, chiefly Connecticut, an attempt was made to obtain a more adequate representation of the flora in all localities. As many plants as practicable were collected and examined for rotifers. This region has been described by Deevey (1940). It is different from Wisconsin in a number of features, and these differences are reflected in the flora. Sphagnum bogs were rare in the regions visited. In Connecticut the lowest pH obtained was 6.0, the highest 9.2, and the median 7.1. For the Wisconsin Lakes studied, the corresponding figures were 3.5-8.5, median 6.8. Within the more restricted range of Connecticut waters few plants showed marked limitation with reference to the median of pH. Exceptions are (1) Sphagnum, which occurred in two mildly acid localities and one mildly alkaline pond to which it had been transplanted, and (2) the Lemnaceae, which occurred more frequently on the alkaline side of the median. The latter observation does not agree with the more extensive collections by Hicks in Ohio (1932), but is descriptive of the Connecticut collections. Plants which occurred most abundantly in the harder, or upper range of bicarbonate were Anacharis, Ceratophyllum, Chara and the Lemnaceae. Some plants grew in much greater numbers in hard water, although they are represented by scattered individuals in softer waters, and show no statistically significant limitation to hard water. This was especially true of Ceratophyllum, Chara, Ranunculus, Anacharis and Gloeotrichia. Plants more common in the softer range were *Utricularia purpurea*, Myriophyllum and Fontinalis. This terminology will be used throughout the discussion that follows; when a species is present in very great numbers in a single collection it will be called abundant, otherwise scarce. But when a species is found in a high proportion of localities investigated, regardless of whether represented by few or by many individuals, it will be called frequent or common, otherwise, rare.

TABLE 8. Distribution of Wisconsin plants with reference to chemistry of water. *Above:* the numbers give the frequency of occurrences above and below the median of various dissolved substances (upper and lower ranges). *Below:* extreme values of pH and bicarbonate in which the groups of plants were found.

Plant	Range	pH	Bicarbonate	Calcium	Magnesium	Residue
Sphagnum...	Upper	0	0	0	0	0
	Lower	12	4	3	3	3
Utricularia...	Upper	11	1	5	3	2
	Lower	26	21	13	14	16
All others....	Upper	25	23	17	16	19
	Lower	3	7	9	7	5
Value of median.......		6.8	28.1	6.3	2.8	48.4

Range in	Sphagnum	Utricularia	All others
pH....................	3.5 - 6.3	4.6 - 8.5	5.6 - 8.4
Bicarbonate (mgm./l.)....	1.8 - 14.6	1.4 - 317.8	3.0 - 317.8

Evidently plants collected in Wisconsin and Connecticut were affected by some chemical factors by which rotifers were also affected. It is now necessary to find out how great an effect the flora of a lake has on the fauna. In the discussion, the words prefer and preference will be used in a descriptive sense to indicate more frequent occurrence of animals on one substrate than on another.

ATTACHMENT OF ROTATORIA TO PLANTS

The problem of substrate preference or limitation is discussed from the standpoint of three different methods of analysis: (1) comparison and contrast of the fauna of different plants, (2) examination of the frequency of attachment of various rotifer species to different substrate plants, and (3) experimental analysis.

FAUNA OF DIFFERENT PLANTS

For this discussion, substrate plants are grouped in a general morphological system, and the fauna of each group discussed. Such a procedure has the advantage of simplifying the discussion and cancelling any errors made by the author in plant taxonomy. The Connecticut data are chiefly used here since the collections were more thorough than elsewhere, and the region is more homogeneous chemically than Wisconsin. The Wisconsin data are used for comparison, confirmation, and to furnish examples of Sphagnum bogs. Utricularia and Sphagnum are treated separately, but other genera are grouped according to the form of the leaf. The groups as defined have no relation to Fassett's Growth Forms. The classification may seem to have no botanical justification, but from the point of view of the rotifer, it seems to work fairly well.

Group 1. Utricularia. Chiefly *U. vulgaris americana*, but includes *U. purpurea*, *U. minor* and *U. intermedia*.

Group 2. Sphagnum. All species collected.

Group 3. Submersed plants, mostly with finely divided, rounded (convex) leaves. Myriophyllum, Nitella, Chara, Proserpinaca (in part), Eleocharis (in part), etc.

Group 4. Submersed plants with predominantly flat or very gently convex leaves, whether finely divided or not. Potamogeton, Ranunculus, Anacharis, Naias, Vallisneria, Lobelia, *Lemna trisulca*, etc.

Group 5. Rooted plants with flat, floating leaves of large expanse. The water lilies and Nymphoides.

Group 6. Free-floating plants. *Lemna minor*, Spirodela.

Group 7. Periphytic colonial algae. Gloetrichia, Coleochaete.

Group 8. Filamentous, green, periphytic algae. Chiefly Oedogoniales.

Group 9. Miscellaneous. All plants, submersed or emersed, not included in the first eight categories including Fontinalis. Chiefly flat forms as Galium, Typha, etc.

Table 9 shows the frequency of attachment of common species of rotifers to these types of plants. The numbers are neither numbers of collections nor of habitats, but are weighted for the number of genera of each type of plant in every locality. All species found in Connecticut during 1940-41 are included. The table can be taken as showing roughly the relative frequency of plant types in lakes in Connecticut and Massachusetts and relative frequency of rotifers on those plant types. Both figures are calculated on the same basis so that faunae of different types may be compared.

The preference of most species for Utricularia is strikingly shown by Table 9. Also, more species of rotifers have been found on this plant than on any of the aggregate groups. Species found especially often on Utricularia may be listed.

Beauchampia crucigera
Collotheca ambigua
campanulata longicaudata
coronetta
corynetis
gracilipes
heptabrachiata diadema
Floscularia decora
melicerta
Octotrocha speciosa
Ptygura barbata
Stephanoceros millsii

All of these species have been found attached to other plants also, but much less frequently. This is especially striking when the relative frequencies of the plant groups are considered. The variety and abundance of the Utricularia fauna is largely due to the species *vulgaris* variety *americana*. *Utricularia purpurea*, collected in 9 New England lakes (accompanied by *vulgaris* in 5), bore ten species, all of which have been found on *vulgaris*. They are listed with the number of times found on *U. purpurea*.

Beauchampia crucigera	1
Collotheca gracilipes	1
ornata	1
trilobata	1
Floscularia conifera	2
janus	2
Ptygura barbata	2
longicornis bispicata	1
crystallina	1
Stephanoceros millsii	2

The Sphagnum fauna raised an interesting question, for it is known that a number of free-swimming rotifers are almost entirely restricted to pools containing the moss (Heinis 1910, Hauer 1935, 1937-38, Myers 1942). Typical examples are *Lecane satyrus*, *Lecane galeata*, *Cephalodella tachyphora*, *Trichocerca rotundata*, *Proales minima*. Since Sphagnum lives almost exclusively in acid water, these species appear to be acidobiont. The attached Sphagnum fauna received considerable attention in Wisconsin, but all species found attached to that moss have also been seen on other plants except three rare species not shown in Table 9. These were *Collotheca sessilis* and *C. cucculata*, each represented by one specimen, and *C. sp.* (Edmondson 1940), represented by two individuals. *Collotheca heptabrachiata* appears in the table as limited to Sphagnum, but the author has seen it on Utricularia in a collection made long before the present study was started, as did Hood (1895). Some species occur very frequently on both Utricularia and Sphagnum, and seem almost confined to the two plants. They are listed.

Collotheca campanulata longicaudata
coronetta
heptabrachiata diadema
ornata
Stephanoceros millsii

A certain number of species seem to favor plants characterized by finely divided, convex leaves (Groups 1 and 3):

TABLE 9. Frequency of attachment of sessile Rotatoria to various types of plants as defined in text. The first figure in each cell refers to collections in Connecticut and southern Massachusetts. The second figure, in parentheses, refers to Wisconsin collections. The frequencies are weighted, so that if a species attached to two genera of the same group in a locality, it was recorded twice for the plant type. The row labelled *collections* gives the total frequencies of the plant types in lakes, similarly weighted.

	PLANT TYPES								
	1	2	3	4	5	6	7	8	9
Collections	38 (47)	3 (14)	78 (57)	88 (29)	27 (8)	17 (–)	48 (–)	48 (–)	51 (–)
COLLOTHECIDAE:									
Collotheca algicola	......	......	......	......	......	......	8 (8)	......	......
ambigua	3 (4)	(1)	......	......	......	......	......	......	......
campanulata	5 (6)	......	2 (3)	2	1	......	......	8 (7)	3
c. longicaudata	1 (5)	(1)	1	......	......	......	......	......	......
coronetta	2 (6)	(1)	1	......	......	......	......	......	......
corynetis	(6)	......	......	......	......	......	......	......	(1)
gracilipes	5 (6)	......	(1)	1	......	......	......	......	......
heptabrachiata	......	(4)	......	......	......	......	......	......	......
h. diadema	(8)	(3)	1	......	......	......	......	......	1
ornata	3 (10)	(3)	3	......	1	1	(1)	2 (2)	2
o. cornuta	6 (15)	1 (3)	1 (3)	5 (2)	4	6	......	1 (2)	2
trilobata	8 (3)	1 (1)	1	2	......	1	......	......	......
Cupelopagis vorax	(5)	......	1	11 (2)	......	4	......	......	3
Stephanoceros fimbriatus	6 (8)	......	4 (6)	2 (1)	......	1	......	......	1
millsii	5 (9)	(1)	1	......	......	......	......	......	......
FLOSCULARIIDAE:									
Beauchampia crucigera	9 (4)	......	4	4	......	1	......	5 (3)	3
Floscularia conifera	15 (11)	1 (1)	14 (2)	7 (1)	8 (1)	2	......	......	9
decora	(5)	(1)	......	......	......	......	......	......	......
janus	9 (6)	......	4 (2)	9 (1)	(1)	......	......	3 (7)	3
melicerta	2 (4)	......	......	3	......	......	......	......	......
ringens	3 (7)	(1)	8	3 (1)	(1)	2	......	......	3
Lacinularia flosculosa	(3)	......	(2)	1	......	......	......	......	......
Limnias ceratophylli	2 (5)	......	(4)	4 (1)	......	1	......	......	5
melicerta	11 (11)	(1)	12 (5)	8 (1)	3 (1)	1	......	......	10
shiawasseensis	......	......	......	1	......	......	......	......	1
Octotrocha speciosa	(10)	......	......	......	......	......	......	......	1
Ptygura barbata	5 (4)	......	......	......	......	......	......	4 (3)	......
beauchampi	1 (10)	1	2 (6)	1	......	1	2 (8)	......	1
brevis	1	(1)	4 (6)	......	......	......	......	......	......
crystallina	5 (12)	......	2 (2)	4	3	3	(1)	5 (2)	5
longicornis bispicata	8 (15)	1 (2)	8 (5)	3	1	......	......	5 (3)	8
melicerta	......	......	......	......	......	......	11 (3)	......	......
m. mucicola	......	......	......	......	......	......	28 (21)	......	......
m. socialis	......	......	......	......	......	......	5 (15)	......	(1)
pedunculata	1 (2)	(1)	(6)	3 (2)	......	......	......	1	1
pilula	10 (18)	(6)	3 (4)	2	2	......	......	3 (3)	4
tacita	1 (1)	......	......	......	......	......	......	......	1(?)
Sinantherina ariprepes	2 (11)	......	2 (1)	3	2	......	......	......	1
socialis	1 (4)	......	2 (1)	5	......	......	......	......	2
Number of rotifer species	31	18	25	21	11	12	7	10	22

Floscularia ringens
Ptygura brevis
pedunculata
pilula
Stephanoceros fimbriatus

On the other hand, flat surfaces (Groups 4 and 5) seem to be adequate or even very suitable for others.

Collotheca ornata cornuta
Cupelopagis vorax
Floscularia conifera
janus
Limnias melicerta
Sinantherina socialis

Although five species have been found on the two genera of algae included in Group 7, *Collotheca algicola* and *Ptygura melicerta* are practically limited to it. Certain species sometimes attach to epiphytic green algae (Group 8), but several have been found attached with both frequence and abundance. They are:

Beauchampia crucigera
Collotheca campanulata
Floscularia janus
Ptygura barbata
longicornis bispicata

In order to indicate more completely the fauna of abundant aquatic plants, all species found attached to certain genera of substrates are listed. The figure after each rotifer name is the percentage occurrence of the rotifer on the plant in collections; that is, the number of times each plant was collected, including

repeated visits to certain localities, was divided into the number of collections in which the rotifer was found on the plant. These figures are based on data from Connecticut and southern Massachusetts during 1940-41 only, and may be taken as roughly proportional to the probability of finding the species on the plants in that region. Species without a number have been found on the plant in other collections. Numbers are rounded to the nearest whole percent. Note that Table 9 is necessarily calculated on a somewhat different basis.

MYRIOPHYLLUM

Beauchampia crucigera	6
Collotheca campanulata	
ornata	6
ornata cornuta	3
trilobata	3
Floscularia conifera	25
janus	12
pedunculata	
ringens	
Lacinularia flosculosa	
Limnias ceratophylli	3
melicerta	6
Ptygura beauchampi	6
brevis	3
crystallina	3
longicornis	3
longicornis bispicata	3
pedunculata	
pilula	6
Sinantherina ariprepes	3
socialis	
Stephanoceros fimbriatus	9
millsii	3

CERATOPHYLLUM

Beauchampia crucigera	4
Collotheca ornata cornuta	
Cupelopagis vorax	4
Floscularia conifera	9
ringens	18
janus	4
Limnias ceratophylli	4
melicerta	22
Ptygura beauchampi	
brevis	9
crystallina	4
longicornis	4
longicornis bispicata	4
pilula	
Sinantherina ariprepes	4
socialis	9
Stephanoceros fimbiatus	4

CHARA

Beauchampia crucigera	10
campanulata longicaudata	5
Collotheca campanulata	5
ornata	
ornata cornuta	5
Floscularia conifera	25
ringens	
Limnias melicerta	25
Ptygura longicornis bispicata	5

NITELLA

Beauchampia crucigera	5
Floscularia conifera	25
janus	10
ringens	5
Limnias melicerta	5
Ptygura longicornis bispicata	20
pilula	5
Stephanoceros fimbriatus	5
millsii	5

POTAMOGETON

Beauchampia crucigera	5
Collotheca campanulata	2
gracilipes	8
ornata cornuta	5
trilobata	2
Cupelopagis vorax	11
Floscularia conifera	17
janus	5
melicerta	3
ringens	3
Limnias ceratophylli	
melicerta	14
myriophylli	3
Ptygura beauchampi	2
crystallina	3
longicornis bispicata	3
pedunculata	8
pilula	2
Sinantherina ariprepes	2
socialis	3
Stephanoceros fimbriatus	3

RANUNCULUS

Collotheca ornata cornuta	10
Cupelopagis vorax	10
Floscularia conifera	10
janus	20
Limnias melicerta	10
cf. shiawasseenesis	10
Sinantherina socialis	10

ANACHARIS

Beauchampia crucigera	4
Collotheca ornata cornuta	4
Cupelopagis vorax	7
Floscularia conifera	4
janus	
ringens	4
Limnias melicerta	7
ceratophylli	4
Ptygura crystallina	7
pedunculata	
pilula	4
Sinantherina socialis	4

FONTINALIS

Beauchampia crucigera	6
Collotheca ambigua	3
ornata cornuta	3
trilobata	
Floscularia conifera	14
janus	8
melicerta	3
Limnias ceratophylli	3
melicerta	14
Pseudoecistes rotifer	

Ptygura longicornis bispicata	3
pilula	3
tacita	3
Sinantherina socialis	6
Stephanoceros millsii	3

It is evident that next to Utricularia, Myriophyllum is the most favorable single genus. Ceratophyllum has always impressed the author as being an especially poor plant for collecting sessile rotifers. While fifteen species have been found on it, they are almost always rather scarce in any collection. Wulfert (1939) lists a number of species attached to Ceratophyllum in a pool where there were no other plants. In connection with the usual poor quality of this plant as a substrate, Edmondson (1940) reported a remarkable situation existing in Boulder Lake, Wisconsin where the reproductive state appeared to be affected by the substrate. As a general rule, the extent of division of the leaf into fine parts is directly correlated with the number of species and individuals attaching.

FREQUENCY OF ATTACHMENT TO SUBSTRATES

Specific Analysis

The preceding pages have shown that each substrate plant type bears a different fauna. We now proceed to examine more closely the species of Rotatoria which attach only to a limited number of plants. The more outstanding examples have been published in preliminary fashion (Edmondson 1940).

Collotheca gracilipes

Collotheca gracilipes (Figure 1A) has been found in about fifteen localities, several times in great abundance. With a few quantitatively insignificant exceptions it is always found attached to *Utricularia vulgaris americana*. In Boulder Lake, Wisconsin, a few specimens were found on Ceratophyllum. Single specimens have been found on *Utricularia purpurea* and *U. intermedia.* Fair numbers have been found on *Potamogeton pusillus* in Bird Preserve Pond, Connecticut, but not nearly in as great abundance as on *Utricularia vulgaris* in the same pond. This pond is carpeted with Chara, but never, in an extensive series of collections, was the rotifer seen attached to that plant. In the Woodbridge Skating Rink pond, Connecticut, the rotifer occurred in such abundance as to give the plants a fuzzy appearance to the naked eye, yet no individual was found atatched to Fontinalis which covers most of the bottom of the pond. On one occasion, 50 moss tips taken within 20 centimeters of the tip of a Utricularia plant were very carefully examined, but no *Collotheca gracilipes* was found. Obviously this rotifer has a very well marked preference for *Utricularia vulgaris*. Moreover, most specimens are found on the fresh, green leaves near the growing tip of the plant. This localized distribution suggests very special reactions to the substrate. The nature of the preference has been examined experimentally, and is reported subsequently.

Ptygura melicerta

The taxonomic status of *Ptygura melicerta* has been discussed before (Edmondson, 1940), so that the details need not be repeated here. It is sufficient to say that in addition to the type, there are two varieties which are well known in the literature. The identity of the type form with Ehrenberg's species is, however, in question.

All three forms of the species have occurred principally in colonies of the alga Gloeotrichia (Cyanophyta), but the two varieties *mucicola* and *socialis* have also been found in colonies of Coleochaete (Chlorophyta). Although the two algae are taxonomically quite different, they are alike in that the colonies consist of radiating thalli, truly branched in Coleochaete, with gelatinous sheaths. The substrate requirements then appear to consist of closely set filaments, sheathed with gelatinous material, and providing spaces in which the rotifers can live. The alga in which *Ptygura melicerta* and its varieties have been most often found is Gloeotrichia. The type form has not yet been seen in Coleochaete, but *P. m. mucicola* has been found in the latter alga four times while *P. m. socialis* has been found there only once. The author knows of no other records of this rotifer on Coleochaete, as Gloeotrichia (Rivularia) is the only published substrate for the species.

There has been only one clear exception to the occurrence in Gloeotrichia or Coleochaete of animals undoubtedly referable to this species. In Taylor Lake, Wisconsin, six specimens were found attached close together on the concave side of a Fontinalis leaf which carried a considerable number of slender Oedogonium and some Bulbochaete thalli. Evidently this situation simulated the requirements well enough to satisfy the reactions of the rotifers. No Gloeotrichia was observed in the collection.

We are now in a position to discuss further the chemical limitations of *Ptygura melicerta*. It will be remembered that *Ptygura melicerta mucicola* has a strong tendency to occur in hard, alkaline waters, *P. m. mucicola* a less strong tendency, while the type form shows no significant limitations to either side of the median value of pH or bicarbonate. This trend is shown graphically in Figures 3 and 4. *P. m. mucicola* has the largest bicorbonate range, and is found at considerably higher values than the other forms, although the upper pH limit is not much different. Since the form can tolerate low bicarbonate concentrations and relatively low pH values, it seems likely that it is found more frequently in hard water because the substrate is more common there. Gloeotrichia, in common with many other blue-green algae can become very abundant in hard water, and is very common in such locations; although it can live in relatively soft water, it is never abundant there, and is rarely found. Therefore, the limitation of this form to hard waters is more a matter of the distribution of substrate than one of direct reaction to the chemical nature of the habitat.

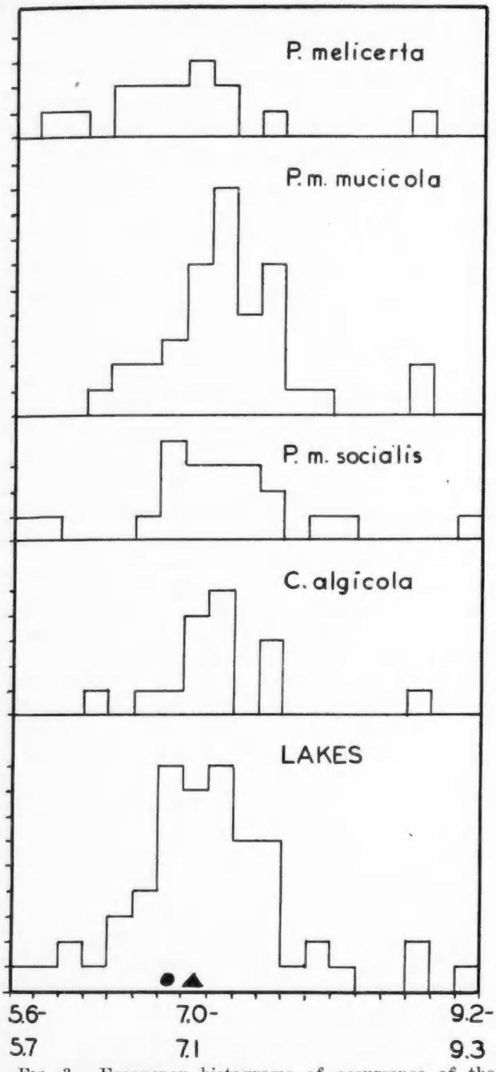

FIG. 3. Frequency histograms of occurrence of the lasiobiontic species of sessile Rotatoria with reference to pH. Each block represents one occurrence in the designated pH range. The distribution of lakes containing at least one lasiobiontic species is shown at the bottom. The triangle shows the location of the median of these lakes, and the circle shows the median of all lakes investigated.

Ptygura melicerta socialis occurs in a much wider range of pH than the other forms, but it is not found in as high bicarbonate concentrations as *P. m. mucicola*. That it can tolerate low pH values is shown by its occurrence in a bog near Presque Isle Lake, Wisconsin at a pH 5.6 (erroneously reported as 3.5 by Edmondson, 1940). From an examination of Figure 4, it seems likely that *socialis* does not show such a strong limitation to the upper part of the bicarbonate range as *mucicola* because it does not tolerate as high concentrations, and is therefore excluded from many hard lakes. It does not appear often at low pH and bicarbonate values because of the relative scarcity of Gloeotrichia there.

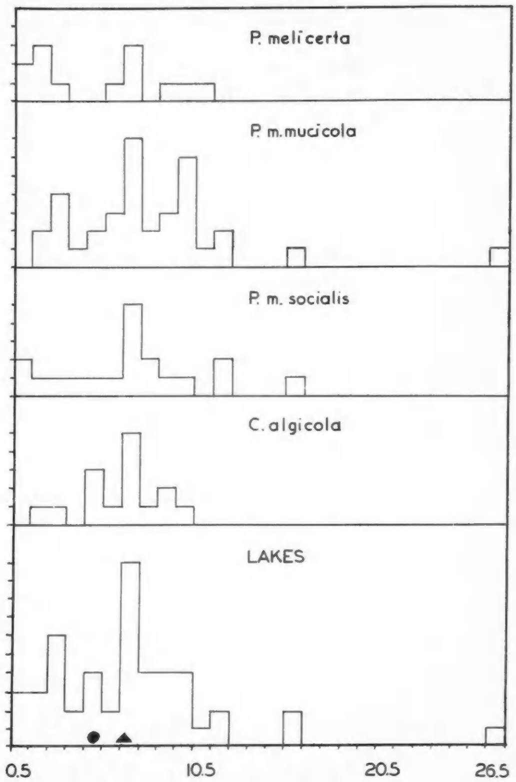

FIG. 4. Frequency histograms of occurrence of the lasiobiontic species with reference to bicarbonate content expressed as alkalinity where 1 unit of alkalinity is equal to 6.1 mgm./l. of bicarbonate. Other explanation as in Figure 3.

This tendency is carried much farther in the type form of the species. While it occurs through a considerably wider range of pH than *mucicola*, the upper limit of bicarbonate is much lower than that of the other two forms. Evidently the type, like variety *mucicola*, is kept out of alkaline lakes by the co-occurrence of bicarbonate, and cannot occur in soft lakes because of the lack of necessary substrate. It will be noticed in Figures 3 and 4 that each form is represented at the highest concentrations by only one occurrence. Nevertheless, the general shape of the distributions confirms the conclusions.

Collotheca algicola

Hudson originally described *Collotheca algicola* as living in colonies of *Rivularia pisum* (now Gloeotrichia) and, as far as the author knows, it has never been found on any other substrate, even Coleochaete. The species can occur in very alkaline waters, but

like the type form of *Ptygura melicerta,* does not tolerate high concentrations of bicarbonate, and so, in spite of its survival at alkaline pH values, is not common in hard water. Figures 3 and 4 show the frequency distribution of *C. algicola* with relation to that of the three forms of *Ptygura melicerta.* It obviously resembles that of the type of *P. melicerta,* and the same explanation of the limited distribution of the species holds good. *Collotheca algicola* and *Ptygura melicerta* type were much rarer than the two varieties of *P. melicerta* (Table 1). This probably is simply a result of sensitivity to both substrate and bicarbonate concentration; the reactions oppose each other, and the number of inhabitable lakes is relatively very small. Symbols at the bottom of Figures 3 and 4 show that the lakes containing this and the previous species are, as a group, harder and more alkaline than the entire set of lakes sampled.

Collotheca campanulata

Although *Collotheca campanulata* (Figure 1E) has been found on a number of substrates, it has attached to epiphytic green algae rather frequently, and in collections, is apt to occur in greatest numbers on epiphytes. On Utricularia and Ceratophyllum, the species usually occurs singly, with the individuals isolated from each other, but on Oedogonium they are often crowded together. On one occasion, 37 animals were attached to a piece 3.6 millimeters long. This species has never been found in great abundance in any lake except in the presence of epiphytes, to which it attached in preference to other substrates.

Floscularia janus

Floscularia janus has been found attached to more kinds of substrate than the previous species, but nevertheless has a strong tendency to attach to epiphytes. It has been collected in very great abundance in five localities, each time in the presence of epiphytes to which the rotifers were attached more often than to other surfaces.

Ptygura barbata

Another species which attaches with some frequency to epiphytic green algae is *Ptygura barbata* (Figure 1F). The only other substrate to which it attached in New England was Utricularia, although Mr. F. J. Myers has found it sparingly on Myriophyllum in Pennsylvania. The species has been particularly abundant in two localities, Bug Lake in Wisconsin and Lake Chaugogagogmanchaugagogchaubunagungamaug in Massachusetts. In both localities, almost all the specimens were attached to epiphytic algae growing on Utricularia, few to the Utricularia itself.

The five species of algicolous rotifers just listed require further discussion. Gloeotrichia colonies can probably be regarded as part of the lasion, since individual thalli are not found. When the alga is abundant, furthermore, colonies may become contiguous over large areas. *Collotheca algicola* and *Ptygura melicerta* are then lasiobionts, in the terminology of Meuche (1939). Stands of Oedogonium included in the present work are regarded as epiphyton in most cases, for only occasionally did they form mats of inter-related thalli on the substrates studied. Therefore *Collotheca campanulata, Ptygura barbata* and *Floscularia janus* are to be regarded as lasiophils. In addition to these, *Beauchampia crucigera* and *Ptygura longicornis bispicata* may become rather abundant on the algae, although attaching freely to other substrates.

The rigorous limitation of the lasiobiontic species to Gloeotrichia and Coleochaete is likely a result of a reaction of larvae to the shape and texture of the surfaces rather than to their chemical nature in view of the wide taxonomic differences in the substrates, especially in view of the exceptional occurrence of *P. m. socialis* among Oedogonium in Taylor Lake. At least one free-swimming rotifer, *Lindia euchromatica* (Edmondson 1938) is limited to Gloeotrichia colonies, having been found in about twenty lakes, invariably associated with the alga. The animals swim only infrequently, when travelling from one colony to another. This and the lasiobiontic species have been found abundantly in *Gloeotrichia echinulata,* which floats in the water, not attached to a substrate. The epiphytophils probably have a thigmokinetic response to highly curved surfaces. Their substrate limitation is much less rigorous than that of the lasiobionts. It might be suspected that rotifers might be forced to attach to epiphytes either as a matter of random distribution to all available surfaces, or that they could not attach to a surface largely obscured by epiphytes, and must therefore attach to the algae themselves. There is evidence against both of these points. In the first place, *Collotheca campanulata* has several times been found to attach predominantly to algae even when the algae were rather scarce and there was plenty of unobscured Utricularia surface available. *Floscularia conifera* was once found fairly abundantly among a thick stand of Oedogonium of the sort favored by *F. janus,* where the latter species would be expected on the algae. Nevertheless, none of the *F. conifera* was attached to algae, every one being directly on the substrate among the algae. This shows that an abundance of epiphytes does not necessarily exclude attachment of large rotifers to the chief substrate.

Cupelopagis vorax

Probably the only sessile rotifer which avoids plants with finely divided, convex leaves in preference for a flat surface is *Cupelopagis vorax.* It has been found most frequently on such plants as Potamogeton and Vallisneria, and on lily pads. This habit very likely has its explanation in the manner of feeding, for Cupelopagis is one of the few Collothecids without long setae radiating from the corona to guide small prey organisms to the mouth. It is a relatively large, depressed organism with a bowl-shaped corona and a flat attachment disc on the

venter which allows a considerable amount of lateral turning (Figure 1C). When small organisms approach, the Cupelopagis turns toward them, and very often they enter the corona where they are trapped. Obviously this rotifer is at an advantage on an extensive, broad surface where there is more chance for small, browsing organisms to approach. It is probable that Cupelopagis larvae have a positive thigmokinetic response to flat surfaces which results in attachment, while the response to highly convex surfaces is to keep swimming. Evidence for this is that on the only occasion when the author found the rotifer in any considerable abundance on Utricularia, almost all of the individuals were attached to the broad sides of the bladders, only occasional specimens being found on the leaves or curved sides of the bladders. On one occasion, more than sixty individuals were found on small quantities of flattened leaves of Potamogeton and Lobelia, but none at all on Utricularia growing in the immediate vicinity (Mt. Carmel, Connecticut, Pond 1).

Ptygura velata

An example of special response to the shape of surfaces is afforded by *Ptygura velata,* which occurred in very great abundance on *Sphagnum erythrocalyx* in a small bog near Trout Lake, Wisconsin. The moss has broad leaves which are deeply curved, with the opposite edges near the tip close together, almost forming a tube. Of the many hundreds of individuals seen (two hundred were counted), every one was attached very near the tip of the leaf, on the concave side, in the tubular part. The animal was almost completely enclosed by the leaf, while only the head projected above the edges (Figure 1D). As many as three individuals lived in a single tip.

In a bog near Presque Isle Lake, Wisconsin, the same rotifer was abundant on a different species of Sphagnum which has long, narrow leaves without curled tips. Here the rotifers attached only to the concave side of the leaves, but anywhere from base to tip. The rotifer has also been found on the concave side and axils of Fontinalis leaves. A single specimen was found in a fork of an unidentified plant of Group 3 in Lake Mendota, Wisconsin. Gosse's original description was from Myriophyllum. Neither he nor other writers have mentioned any such limitations of attachment. The Wisconsin species agrees as well as can be expected with Gosse's description of *P. velata,* but there has been some confusion in the literature about the characteristics of the species, and the taxonomic situation is not closed.

Collotheca ornata var. *cornuta*

Collotheca ornata cornuta shows a peculiar sort of substrate preference in that it is often found in great numbers on the under side of *Lemna minor* and *Spirodela polyrhiza,* although it attaches freely to Utricularia and other plants. In 17 collections of these plants in 11 locations in New England during 1941, the rotifer was found 11 times, in 6 localities. This is a considerably higher incidence than on any other plant collected a comparable number of times. The distribution on the plants shows a considerable hyperdispersion (Gause 1936), for while many plants have more than 30 individuals, most have none at all. Apparently the young which hatch in such a situation do not swim far, for this is true even in thickly packed beds of the plants.

Ptygura brevis

A species apparently referable to *Ptygura brevis* (Rousselet 1895) was found in 12 localities in Wisconsin and Connecticut, and showed a very special substrate preference. Every time the species occurred on Ceratophyllum (5 localities), all specimens were found in the forks of leaves (Figure 1B). Even in Ball Pond, Connecticut where the species were abundant, all specimens were in forks, and almost every fork of several plants examined was occupied by one, two or three rotifers; none was seen on the sides of leaves or on other plants. The species has been taken only in isolated specimens on other plants elsewhere; 1 specimen in a fork of Utricularia leaf, 2 in Myriophyllum forks, and 1 on the side of a Utricularia leaf. Two specimens were found on Megalodonta wedged between the side of a leaf and a colony of Gloeotrichia. The only time the species occurred in fair quantity anywhere but in the forks of Ceratophyllum was in a bog near Presque Isle Lake, Wisconsin on the concave side of Sphagnum leaves.

Apparently *Ptygura brevis* is strongly attracted by negatively curved surfaces, such as forks of leaves, where curvature is concave in one direction, convex at right angles to that, although plain concave surfaces will be tolerated in the absence of forks. Possibly the species studied is not the same as described by Rousselet from England, but it fits the description well. Literature records the species from Myriophyllum, Ranunculus and Ceratophyllum, but no mention has been made of a limitation to forks.

Ptygura beauchampi

Ptygura beauchampi presents a puzzling problem which can only be stated without solution. The species was originally found and recorded without naming by de Beauchamp (1932) on the lateral, concave surfaces of shells of Planorbid snails. The present author has found it on a variety of substrates including snail shells where it usually occurs in groups, and in Gloeotrichia where tube formation is partly suppressed, the foot projecting far beyond the bottom of the tube. The remarkable thing is that, in any given locality, the rotifer is apt to attach to one substrate exclusively, while in another locality it attaches to something else, also exclusively. Examples may be given. In three different lakes in southern Wisconsin, it was found on snail shells, but nothing else. In two localities it occurred on the trapdoor valve of Utricularia bladders, but nowhere else on

the leaves or stem of the same plants. In one of these places, 96 specimens were counted on a portion of Utricularia; all were attached to valves in groups of four, five or six. While this is not a very great number of individuals and observations, it and the collecting conditions are such that the results cannot be attributed to statistical or sampling accidents.

As far as the author could see, there were no morphological differences between specimens from different substrates. Other species have occasionally shown similar tendencies, but never to the extent exhibited by *P. beauchampi*. For instance, *P. longicornis bispicata*, which ordinarily attaches to a number of substrates in a given locality, has on occasion been found to limit itself almost exclusively to epiphytic green algae, even though the rotifer was abundant.

EXPERIMENTAL ANALYSIS

Attempts were made to discover by experimental means the factors which operate in some of the examples of substrate preference described in the preceding section, and the extent of their influence. The technique was simple. Small (9 cc.) Stender dishes were filled with pond water. Small pieces of leaves of two or more different plants were placed in the dish. There were no rotifers of any kind on these pieces, nor any considerable amount of epiphytic organisms. Ordinarily the pieces were made as nearly equal in area as possible, but when it was known that the rotifer being studied showed a strong preference for one of the plants, an excess of the other plant was used, generally about twice the area. Finally, many reproducing adults of the rotifer were added. These were attached to very small pieces of substrate which had been trimmed with iridectomy scissors. In this way, any tendency towards sociality with the adults was minimized or excluded.

All experimental dishes were kept in a damp chamber, in diffuse light, as long as any reproduction was taking place. Experiments usually ran two or three days. The newly attached rotifers on each plant fragment were counted every day, and water changed in order to keep chemical conditions favorable. Most plant fragments remained green and fresh under such conditions, especially those of Utricularia, Nitella and Chara, particularly if the latter two were cut as close to the cell cross walls as possible to minimize loss of cytoplasm to the water. Occasionally they grew a little, and Utricularia sometimes even put out rudimentary growing buds. Some dishes were spoiled by excessive growth of bacteria and fungi, but usually remained fresh for as long as the experiment was continued. Sometimes rotifer eggs failed to hatch, even in very fresh cultures, and even when the adults possessed plenty of eggs at the beginning.

If the rotifer under consideration shows no preference for either substrate, the number of young attaching to each piece should be proportional to the area. If there is a preference for one kind of plant, this will be expressed by a greater number of attachments to it, and the degree of preference can be expressed in terms of the percentage attaching to each plant, or by difference between the number attaching and the number expected if there were no preference. An exact statistical analysis of experiments of this sort is difficult since they were performed on a semiquantitative basis; the areas of the plants were rarely measured, and it is known only that two plants were represented by approximately equal areas or that there was at least twice as much of one as the other. Yet, under the conditions described, a good idea of the significance of the results can be obtained by assuming that equal numbers should attach to each substrate. Since the experiments were always set up with equal amounts of substrate or with excess of the unfavored one, this procedure has the effect of reducing the apparent effect of substrate preference. Therefore, any preferences that can be observed are surely real. Under the conditions of observation and recording, it is most unlikely that spurious substrate preferences would appear. The differences between expected and observed attachments to each kind of substrate were tested by chi-square using the usual criteria of significance. All differences given in tables are significant unless otherwise stated. It should be pointed out that the statistical reliability of such experiments is to be achieved better by having a greater number of attachments in a smaller number of experiments than by having many experiments with only a few attachments in each, as long as there is no overcrowding.

Collotheca gracilipes

The most extensive series was performed with *Collotheca gracilipes* which, in nature, shows a very strong preference for young leaves of *Utricularia vulgaris americana*. This series consists of three groups; the first tested the preference between two different kinds of plants, the second tested the preference between young and old Utricularia leaves, while the third tested the preference between fresh and chemically modified Utricularia leaves in an attempt to discover the qualitative difference between leaves to which rotifers react.

Table 10 shows the results of the first group. The total number of rotifers attaching to each substrate in fifteen pairs is given. Certain experiments need elaboration.

The largest set of substrates was performed with Chara and Utricularia. In 11 of the 13 experiments the attachments were

to Utricularia	48
Chara	1
Bulbochaete on Chara	2
Debris on Chara	2
Glass bottom of dish	9

Although Utricularia was by far the least available substrate, except epiphytes and debris, it was used by almost 80% of the young animals. Only a single specimen attached to Chara. The animals which at-

TABLE 10. Results of experiments on the substrate preference of *Collotheca gracilipes*, showing the total number of rotifers attaching to different substrates in the number of experiments indicated. Explanation in text.

Substrates	Number attaching to each	Number of experiments
Utricularia	182	13
Chara	1	
Other	13	
Utricularia	48	1
Nitella	0	
Utricularia	30	2
Fontinalis	6	
Utricularia	23	1
Sphagnum	1	
Utricularia	136	5
Ceratophyllum	29	
Utricularia	84	2
Naias	6	
Utricularia	+	1
Vallisneria	0	
Utricularia	78	3
Anacharis	29	
Utricularia	135	1
Eleocharis	11	
Utricularia	4*	2
Ranunculus	1	
Utricularia	19*	2
Potamogeton pusillus	27	
Utricularia	33	2
Spirodela	66	
Utricularia	128*	6
Myriophyllum	108	
Utricularia	157	4
U. purpurea	3	
Utricularia	111	4
U. intermedia	78	

*Not significant differences.

tached to glass did so only in two experiments where the only Utricularia available was a few small pieces introduced with reproducing adults. Evidently the rotifers will attach to glass in preference to Chara, but only if Utricularia is unavailable. In two other experiments where Chara and Utricularia were both represented by very fresh, clean portions from near the tip of plants, 134 individuals attached to Utricularia, none to Chara. Thus Chara is definitely shunned by *Collotheca gracilipes*. Since Chara produces a volatile, highly odorous compound, it was thought that part of the basis for avoidance of Chara was a reaction to that substance. Yet, when a piece of Chara was boiled violently in pond water for several minutes and rinsed well, it was still rejected by rotifers, although 34 individuals attached to Utricularia (1 experiment). It is possible, of course, that the substance was not completely removed.

In experiments with Fontinalis and Utricularia, some rotifers attached to the moss, but only to young green leaves near the growing tip. Ceratophyllum was not as favorable as suggested by figures in Table 12, for of the 29 animals attaching to it, 27 did so

TABLE 11. Results of experiments on the selection by *Collotheca gracilipes* of modified *Utricularia* substrates. Experiments described in text.

Experiment	Substrate	Number of Attachments
SERIES A:		
1	Fresh	81
	Modified	22
2	Fresh	35
	Modified	20
3	Fresh	55
	Modified	32
4	Fresh	154
	Modified	90
Total 1-4	Fresh	325
	Modified	164
5	Fresh	105
	Modified	1
SERIES B:		
6	Fresh	30
	Modified	1
7	Fresh	76
	Modified	49

TABLE 12. Results of experiments on the substrate preference of *Floscularia conifera*.

Substrates	Number attaching to each	Number of experiments
Utricularia	5*	1
Chara	2	
Utricularia	98	2
Ceratophyllum	27	
Utricularia	42	1
Sphagnum	4	
Utricularia	14	2
Myriophyllum	20	
U. purpurea	7	
Utricularia	106	1
Potamogeton pusillus	15	
Chara	43	
Utricularia	38	1
Nitella	10	
Utricularia, young	29	1
Utricularia, old	17*	

*Not significant differences

in one experiment where the material consisted of young parts from near the tip of the plant. In this experiment, 42 attached to Utricularia.

Other plants relatively unsuitable for *Collotheca gracilipes* are Nitella, Sphagnum, Naias, Vallisneria, Anacharis, and Eleocharis. While considerable numbers attached to Anacharis, these were all on very young tip parts when the only alternative was rather old Utricularia leaves.

Collotheca gracilipes in most experiments did not attach to glass, although the area of the dishes was considerably in excess of any plant used. But in one group of experiments using fresh and modified Utricularia leaves, about 100 individuals attached to glass while 500 attached to a smaller area of Utricularia. There is obviously a preference for Utricularia still, but under some circumstances the rotifer can attach readily to glass. The author knows of no possible differences in the experiments which could account for this, for the technique was uniform throughout. In order to see whether the presence of periphytic bacteria has an effect on rotifer attachment to glass, rotifers were offered cleaned, flamed glass rods, glass rods coated with bacteria, and a small piece of Utricularia as control. More than 100 attached to the Utricularia indicating abundant production of larvae, but none to either kind of glass rod. The only conclusion to be drawn from this negative experiment is that probably neither presence nor absence of bacteria is a critical substrate requirement.

Under experimental conditions *Collotheca gracilipes* attached in abundance to certain plants in addition to Utricularia. Fair numbers have been found on *Potamogeton pusillus* in Bird Preserve Pond, and it is of some interest to observe the readiness with which it attaches to the plant in experiments. In the two experiments, there was a greater area of Potamogeton available. In an unsatisfactory experiment with *P. robbinsi*, 3 attached to Utricularia, 1 to Potamogeton. Contradictory results were obtained in two experiments with Spirodela. In one, 24 animals attached to Utricularia, none to Spirodela. In the other, 9 attached to Utricularia, 60 to roots of Spirodela and 6 to leaves. Myriophyllum is obviously suitable for *Collotheca gracilipes*. In three experiments, 23 attached to Utricularia, 67 to Myriophylllum. The Myriophyllum used in these three experiments had been kept for about five months in an aquarium and was very fresh and clean in appearance. In the other three experiments it had been recently collected, and was rather coarse in appearance.

Further experiments were performed with equal areas of different species of Utricularia. Table 10 shows that *U. vulgaris* is preferred to *U. intermedia* and *U. purpurea*, especially the latter. *Collotheca gracilipes* has been found on each just once in nature, each time represented by one individual. *U. purpurea* has curved processes on the epidermal cells which give the plant a rather rough surface, and it may be this which makes it such an unsatisfactory substrate, but there is no such obvious explanation for the relative unsuitability of *U. intermedia*, for the surface is almost always smooth and clean.

The results of the first group of experiments, given in Table 10, may be summarized briefly in the statement that while *Collotheca gracilipes* favors *Utricularia vulgaris americana* over most other substrates under experimental conditions, some other plants, such as *Potamogeton pusillus*, Myriophyllum, Spirodela and the young but not old leaves of Ceratophyllum, are fairly satisfactory.

Utricularia leaves of different age.—Since *Collotheca gracilipes*, in nature, occurs with greatest frequency on the young leaves near the growing tip of *Utricularia vulgaris americana*, it seemed advisable to test this preference under experimental conditions to see if the phenomenon is a result of orientation of the plants, or if there is a difference in the quality of leaves of different age to which rotifer larvae react. Six experiments were performed in the manner described before. Young leaves were taken from near the growing bud of plants, separated from it by no more than three leaves. Old leaves were selected well back on the plant, between the twentieth and twenty-fifth from the bud. In these experiments, 89 animals attached to young leaves and only 23 to a greater area of old leaves. This is certainly a significant difference, and there is probably a qualitative difference between the leaves. The number of animals attached to old leaves divided by the number on young leaves gives a ratio of 0.26.

Fresh and modified Utricularia leaves.—Next an attempt was made to determine the nature of the difference between leaves of varying age. Experiments were made with leaves modified in various ways to see what effect modification had on the reaction of rotifers. Since the difference could depend either on chemical properties of the leaf or on the minute physical configuration of the surface, experimental leaves were treated in ways which would alter at least one, then offered to the rotifer larvae with a fresh piece as control. Two series of experiments were made. The results are shown in Table 11. A preliminary note has been published (Edmondson 1941).

Series A. This series was made using only leaves from near the tip of Utricularia separated from the bud by no more than five leaves. Pieces of such leaves were subjected to the treatments described.

Experiment 1. Leaves were boiled in pond water for two minutes. A portion of boiled leaf was matched against an equal area of fresh leaf.

Experiment 2. As in 1, but using ethyl alcohol.

Experiment 3. As in 1, but using ethyl ether.

Experiment 4. As in 1, but using acetone.

The results as shown in Table 11 are similar. In all, more animals attached to the unmodified leaves than to modified ones, but considerable numbers attached to the latter, showing that their suitability was not completely destroyed. The ratio of the number on modified leaves to that on fresh leaves is 0.50, or about twice as large as the ratio between young and old leaves. This may be interpreted to mean

that boiled, young leaves are twice as good as old, fresh ones. The various treatments caused a great wrinkling of the surface and other extensive disturbances of its physical structure, and might have been supposed *a priori* to reduce the suitability of the leaf more than the much less evident changes accompanying natural aging.

Experiment 5. A piece of leaf was soaked in warm, strong NaCl solution for five minutes, rinsed and soaked in pond water. Only one rotifer attached to this leaf. Just what difference there is in the effect on the leaf between this and other treatments is unknown; the experiment makes no positive contribution to the series.

The first four experiments in Series A seem to indicate that the rotifer larvae do not react positively to some character possessed by the young leaves. The solvents would be expected to remove any ordinary compounds which might attract larvae and negate any special physical qualities of the surface. Therefore, it seems likely that older leaves possess some quality which repels larvae to young leaves which lack it. At this stage it appeared to the author that a pectin, or some similar substance formed as leaves age, were the responsible factor. For this reason, a number of experiments was made with ammonium oxalate solution, which liberates pectins from cell walls of plants. Unfortunately, by this time only very unsatisfactory Collotheca material was available; the only population which could be found had started sexual reproduction, so that only a limited number of amictic, female producing eggs was available. An extensive series of experiments with controls was set up; many of these were sterile, and only two were successful enough to consider further.

SERIES B. Old leaves were boiled in 0.5% ammonium oxalate solution, rinsed thoroughly in pond water, and matched against equal areas of fresh, young leaf.

Experiment 6. The old leaf was boiled for two minutes. Thirty animals attached to fresh leaf, 1 to old.

Experiment 7. The old leaf was boiled for ten minutes. The fresh leaf had 76 animals, the old one 49. The ratio of number on boiled leaf to that on fresh leaf is 0.64.

These last two experiments, inadequate as they are statistically, suggest that the pectin hypothesis is correct, since when the leaf is boiled in a substance known to dissolve pectins, it was more suitable to the rotifers than when it had not been boiled at all, as measured against fresh, young leaf as standard. This can be seen by comparing the ratios.

$$\frac{\text{Number on old, fresh}}{\text{Number on young, fresh}} = 0.26$$

$$\frac{\text{Number on young, modified}}{\text{Number on young, fresh}} = 0.50$$

$$\frac{\text{Number on old, modified}}{\text{Number on young, fresh}} = 0.64$$

In fact, modified, old leaf is somewhat better than modified, young leaf, probably because of its firmer structure. In one of the unsuccessful control experiments in which old leaf, boiled in ammonium oxalate solution, was matched against unmodified, old leaf, only two animals were produced, but both attached to the boiled leaf as would be expected.

On the basis of information at hand, it may be said that *Collotheca gracilipes* larvae seem to react negatively to a substance, soluble in weak ammonium oxalate solution, which is secreted by plant cells as they age; this substance is probably a pectin. Further research along the lines suggested above, and with experiments in which young leaves are modified by pectin preparations, should settle the problem. The pectin hypothesis would explain the distribution of *Collotheca gracilipes* on *Utricularia vulgaris americana* plants, but would not explain the infrequency of attachment to such pectin free surfaces as glass. The tendency to attach to tip parts of other genera of plants such as Ceratophyllum and Fontinalis are probably of significance in this connection, but there is at present no explanation for the superiority of Utricularia for this rotifer, or indeed, for sessile rotifers in general. It is doubtful that the general quantity and quality of the epiphytic fauna is determined by pectin-like substances.

Floscularia conifera

Floscularia conifera was found in abundance on a number of substrates, including Chara, in Bird Preserve Pond at Woodbridge, Connecticut at the same time *Collotheca gracilipes* was abundant in 1940. It seemed advisable to experiment with this species, both as an example of a less discriminate species and as a general control to the Collotheca experiments. In experiments, it attached to many kinds of substrate freely, yet it showed a quantitative preference for certain ones. Table 12 gives the data.

Data in the table show a slight but statistically insignificant preference for Utricularia over Chara even though Chara is freely used as substrate in nature. Although there were by far too few animals in the experiment to show the preference definitely, it is substantiated by field data from the Bird Preserve Pond on June 27, 1940. There were 6.9 rotifers per square centimeter of Chara, but 9.5 per square centimeter of Utricularia. The methods of making such determinations as well as further data on the quantitative seasonal abundance of sessile rotifers will be given in Part II of the present studies.

Other experiments listed in Table 12 show that Utricularia is preferred to other plants except Myriophyllum which is at least as acceptable. Experimental results agree rather well with field data on the frequency of attachment to the plants used. This fact makes it probable that the technique of experi-

mentation is capable of exposing real substrate preferences, and that the experiments on *Collotheca gracilipes* are generally valid.

An experiment with young and old Utricularia leaves (Table 12) revealed a certain preference for the young ones. In nature, this expresses itself only weakly, but in a definite, systematic way as will be seen in Part II in a detailed study of dynamics of natural Floscularia populations. No experiments were made with ammonium oxalate.

Ptygura brevis

As shown before, this animal is chiefly found in the forks of Ceratophyllum leaves. In one experiment, the substrates offered were a piece of Ceratophyllum with six unoccupied forks and a piece of Ranunculus with seven unoccupied forks. In twenty-four hours, five forks of each plant were occupied with young Ptygurae. The experiment shows that a tendency to live in forks is elicited by Ranunculus as well as by Ceratophyllum.

OPTIMAL SUBSTRATES

Occasionally, some species have been found in enormous numbers. As may be expected, species which are indiscriminate in choice of substrate usually form large populations on a great many plants, while those that are selective will be found only on the favored plants while others are left almost bare. *Collotheca gracilipes* has been found three times in great numbers, and in each case, all specimens were on Utricularia but no other plant. Species which appear fairly nonselective in a series of collections may yet attach principally to only one plant when very abundant. The best examples are *Collotheca campanulata* and *Floscularia janus* on epiphytes. These two species have never been found in great numbers except in the presence of epiphytes, to which the vast majority of the rotifers were attached.

EFFECT OF PLANT SUCCESSION ON THE ROTIFER FAUNA

Now that it has been shown that the fauna of several plants is different, and that some species of rotifers are highly restricted in their choice of substrate, we may speculate as to whether there is a succession in the rotifer fauna parallel to that in the flora.

The study of plant succession, judged by a series of lakes in different stages and by different parts of the same lake, has been benefited by the attention of Pearsall (1920, 1921) who demonstrated, in the English Lake District, a correlation between the percentage of organic matter in bottom deposits, flora, and to some extent, chemistry of the water. L. R. Wilson (1935, 1937, 1941) studied extensively the distribution of plants within a number of Wisconsin lakes and related it to the character of the bottom, as did Rickett (1922, 1924). It is impractical to review here the content of these papers, but reference is made to the 1939 paper by Wilson for a general summary, and to the recent paper by Hutchinson (1942) which gives a brief account of the developmental processes of lakes, following work on Connecticut lakes including that of Deevey (1942) on the history of Linsley Pond. The nature of aquatic plant succession as it applies to the present paper may, however, be briefly outlined as follows.

As a lake matures and fills up with endogenous and exogenous deposits, there is a progressive series of changes in the chemical nature of the bottom material, and the water, and in the flora. The exact course and final results of the succession depend on the nature of the surrounding terrain (paralimnion), original shape and size of the basin, character of the drainage and the climate. In general the flora is very sparse at first, but becomes larger and more varied as the bottom deposits grow richer in organic matter. Eventually there comes a time when the number of plant types is reduced, and the lake passes into swamp or bog stages. Naturally bays of irregular lakes fill faster, and plant succession in such parts may be well ahead of the rest of the lake.

There has been very little work on changes of fauna accompanying plant succession. Macan (1938) studied the distribution of Corixidae (Insecta: Hemiptera) in a large number of habitats with reference to stage of floral development. He found a close correlation between organic content of bottom and the bug fauna, this paralleling plant development. He could demonstrate at least two distinct successional series. Hutchinson (1940) discussed the possibility of succession in Indian Corixids.

Now in considering the sessile Rotatoria, it must be held in mind that any succession of species must be affected both by the flora and by the chemistry of the water, both of which are related to the nature of the bottom. This will introduce a certain amount of variation which will obscure the relationships. For instance, if there is a probability of 0.80 that a certain plant will occur on a certain kind of bottom, and a probability of 0.70 that a certain species of rotifer will be found on that plant, then the probability of getting the rotifer and bottom type associated is only 0.56, and field data might not reveal a significant correlation. In nature the initial probabilities are much lower and there are usually more than two variables; each new variable introduces further uncertainty. Nevertheless, an attempt to establish a rotifer succession is certainly worth while. Unfortunately, there are not yet data on the organic content of the bottoms of all habitats studied, and it is not practicable to establish a series such as Macan set up for Corixidae. Yet, from known facts, a general outline can be given in terms of flora and chemistry.

As more, and different plants enter a lake during its development, the potential rotifer fauna is correspondingly increased. The lists of the fauna of several plants given previously show in a general way what to expect in specific instances, and may be used in any system of plant succession. Isoetes, Nitella and certain algae appear in quite early

stages, but such plants bear a scanty fauna, as do other rosette types which live on bottoms with little organic matter. As Myriophyllum and certain other plants enter in intermediate stages, the fauna is potentially increased very greatly. However, as development proceeds, the flora is reduced in older stages, leaving chiefly plants with floating leaves and those of the rosette type. Most of the former would be included in our Group 4 (page 47), the latter in Group 5. Neither group bears an extensive fauna. But as this reduction occurs, or perhaps sometime before it starts, the location may become suitable for Utricularia which brings with it a very large potential fauna. Moreover, many seepage lakes pass into Sphagnum bog stages, and this single genus bears a fauna almost as extensive as all of Group 4. Thus, with progressive aging of a lake, the sessile rotifer fauna becomes more varied, although it is very likely that for a very great part of the succession the fauna is fairly stable. Removal of forms with flexuous stems and divided leaves such as Myriophyllum and some flat leaved forms does represent a definite loss, and makes the probability of finding certain species smaller.

Progressive chemical changes of course affect the fauna; sometimes these may accentuate, at other times counterbalance floral effects. For instance, *Cupelopagis vorax* may become abundant on water lily leaves in alkaline water, but since the rotifer is rare and never abundant in soft, acid waters, lily leaves in acid bogs do not bear this species. In general, the rotifer fauna of hard water is less varied than that of soft water, so that the Utricularia fauna is apt to be relatively poorer in hard water although Utricularia may be an important element in the flora of alkaline ponds and bays.

Unlike many groups of organisms (Deevey 1942), rotifers apparently leave no persistent microfossils, so there is no direct historical evidence for the scheme outlined. But since different successional stages can occur in different parts of one lake, the effect of flora can be studied to some extent in the same body of water. As an extreme example, Lake Pocotopaug may be chosen. Two parts of the lake were studied on several occasions, and the results shown in Table 13. This large shallow lake has a sparse vegetation along the western side in water about three meters deep. The bottom is rather sandy and has a small amount of Nitella, Eleocharis, Potamogeton and Naias in isolated clumps. There is a small embayment on the western side which is almost closed off by a ridge of sand. The embayment is about thirty meters long, eight meters wide, and about a meter and a half deep. The mouth into the lake is about two meters across and half a meter deep. The bottom of the bay is evidently rich in organic material, judging from its appearance, and has an abundant flora. There are ten plants in the main lake including the two recorded substrate algae and nine in the bay, of which five are common to bay and lake. If complete collections and specific determinations had been made, the number of species in the bay certainly would have been the larger.

TABLE 13. Distribution of substrates and sessile Rotatoria Lake Pocotopaug. Presence of organism in bay or lake is signified by an X. Description in text.

	Bay	Lake
SUBSTRATES:		
Nitella		X
Eleocharis		X
Gloeotrichia		X
Vallisneria		X
Lobelia		X
Vaucheria	X	X
Naias	X	X
Coloechaete	X	X
Potamogeton sp. 1	X	X
Fontinalis	X	X
Myriophyllum	X	
Lily pads	X	
Potamogeton sp. 2	X	
Hypericum	X	
ROTATORIA:		
Collotheca trilobata		X
Ptygura melicerta		X
Ptygura melicerta socialis	X	X
Beauchampia crucigera	X	X
Ptygura melicerta mucicola	X	
Collotheca campanulata	X	
ornata	X	
ornata cornuta	X	
Floscularia conifera	X	
ringens	X	
Limnias shiawasseensis	X	
Ptygura longicornis bispicata	X	
Ptygura crystallina	X	
pilula	X	
Stephanoceros fimbriatus	X	

The rotifer fauna consists of four species in the lake and thirteen in the bay, of which only two are common to both. One of the lake species is *Ptygura melicerta* which can live only in Gloeotrichia, and is necessarily limited to the lake since that alga does not occur in the bay. While this is an extreme example of unequal distribution between two parts of a lake, the same thing can be observed in bays with wide, deep openings.

EFFECT OF HABITAT SIZE ON THE ROTIFER FAUNA

As lakes age and become filled with sediments, they grow smaller, and various changes associated with size take place which can affect the fauna. The amount of wave action is reduced with smaller size, and the presence of thick beds of vegetation reduces this even further (Meschkat 1934). The measurement of size used here is quite subjective, but it is used consistently. Actually two things are involved, the volume of water in the locality and the quantitative and spatial relation of plants to that volume. On this basis, lakes studied in Connecticut and Massachusetts may be divided into three groups:

1. Large localities, with relatively little vegetation and large surface area. Circulation of water is free.
   Bantam L., Spectacle Pond, Winchester Pond, Moodus Reservoir, Lake Zoar, East L., East Twin L., Beseck L., Waramaug L., Ball Pond, Little Pond, Silver L., Cedar Swamp L., Upper Pond Lily, Pocotopaug L., Candlewood L., Linsley Pond, Taunton Pond.

2. Intermediate localities; smaller, with considerable masses of submersed vegetation, or the lake so arranged that it is not subject to much wind action, or protected bays of larger lakes.
   Quonnipaug L. (bay), Quassapaug L. (protected portion), Congamond Pond, Totoket Backwash, Pomperaug Pond, Little L., Bashan Reservoir, West Pond, Lake Chaugogagogmanchaugagogchaubunagungamaug (also known as L. Chaubunagungamaug or Webster L.), Black Pond, Highland L.

3. Small localities, with massed vegetation, or well protected from wind.
   Mohawk Pond, Pocotopaug L. (bay), three unnamed ponds on Route 80, Upper and Lower South Meadow Ponds, Lyd Hyt Pond, Bird Preserve Pond, six unnamed ponds at Mt. Carmel, Pool near Quassapaug L., Pond at Edgewood Park, New Haven, Woodbridge Skating Rink, Five Mile Pond, Pocotopaug Pond.

The two families of rotifers treated in this paper show considerable differences in their distribution among the three types of habitat so defined. Table 14 shows the frequency of species of the families in different habitats. The data are shown graphically in Figure 5. Collothecidae are practically excluded from large localities, the largest number of species ever found in one large lake being four. As many as 9 species of Collothecidae have been found in small localities. On the other hand, Flosculariidae are more evenly distributed. The difference between the distributions of the two families can best be seen by comparing the mean number of species in each habitat type.

TABLE 14. Frequency distribution of numbers of species of Collothecidae and Flosculariidae in large (L), medium (M) and small (S) localities. The mean number of species is calculated including frequencies of O species. See Fig. 5.

Number of Species	Number of lakes with given number of species					
	Collothecidae			Flosculariidae		
	L	M	S	L	M	S
0	12	3	3	0	1	0
1	5	4	1	4	0	3
2	0	2	4	4	2	3
3	0	0	4	3	1	2
4	1	0	2	3	2	3
5		1	0	1	4	0
6		0	3	1	0	2
7		1	1	1	0	3
8			1	0	0	1
9				0	0	2
10				1	0	
11					0	
12					1	
Mean number of species	0.5	1.1	3.3	3.4	4.3	4.5

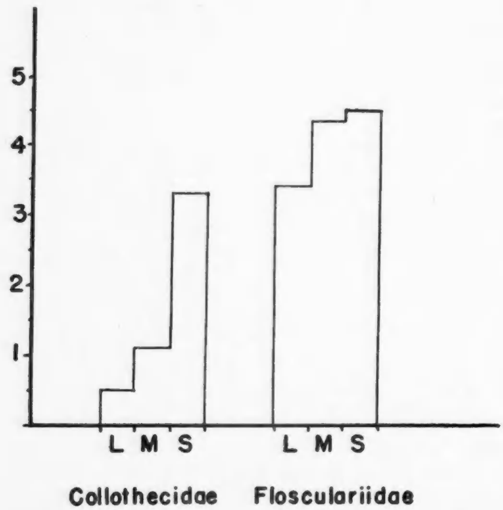

FIG. 5. The mean numbers of species of the two families of sessile Rotatoria in habitats of different size as described in the text; large (L), medium (M) and small (S).

The explanation probably lies in differences in feeding. Flosculariidae, like most of the more familiar rotifers, have an extensively ciliated corona which makes currents in the water, bringing food organisms to the mouth. Collothecids, on the other hand, have the ciliation greatly reduced or absent so that perceptible currents are usually not developed. Instead, most species have long, extremely fine setae extending out from the corona (Figure 1A, E). When small organisms such as minute ciliates come into contact with the setae, they very often follow them right down to the corona where they are swallowed. It seems most likely that such an apparatus would not function well in a current of water, or in localities where wave action would displace the setae and prevent feeding. The amount and kind of food which can develop in habitats of different size must have an effect also, and probably would accentuate the direct effect. It might be suspected that Utricularia, which is limited to quiet waters, might be responsible for the faunal differences, but examination of Table 9 shows that more than half the species living on Utricularia are Flosculariids, so the plant cannot bring a predominance of Collothecids into small habitats. Thus the qualitative nature of the fauna of sessile Rotatoria is fundamentally affected by physical factors associated with habitat size, one of these being the quantitative development of vegetation.

REGIONAL DIFFERENCES IN THE FAUNA

Deevey (1940) discussed the features of the four physiographic provinces of Connecticut and showed that the waters of each region taken as a group are different limnologically. Since sessile Rotatoria were collected from a number of localities in the three largest regions, it is of interest to see if the rotifer fauna shows any differential distribution which can be correlated with limnological differences. Table 15 shows the number of lakes sampled in each province of Connecticut and Massachusetts and the number of times that a number of rotifer species and substrates occurred in each province. Chemical data are given showing that lakes of the eastern highland are softer and more acid than those of the other two regions. Lakes of the central lowland and western highland have the same mean pH, but bicarbonate concentration is higher in the former. Thus each region is clearly distinct with reference to pH and bicarbonate. The table shows also that each region has a distinct fauna with reference to the frequency with which various species were collected. It should be borne in mind that each region is represented by a different number of lakes.

TABLE 15. Distribution of some sessile Rotatoria and substrate plants found in Connecticut and southern Massachusetts. The figures give the number of occurrences in each physiographical region.

	Province		
	Western	Central	Eastern
Number of lakes	20	16	12
Beauchampia crucigera	6	5	3
Collotheca algicola	3	2	2
campanulata	6	2	3
gracilipes	5	0	0
ornata	5	2	2
ornata cornuta	7	10	3
trilobata	3	3	2
Cupelopagis vorax	1	8	2
Floscularia conifera	10	3	7
janus	10	0	1
ringens	2	6	2
Limnias ceratophylli	5	2	0
melicerta	9	10	3
Ptygura barbata	3	1	1
beauchampi	3	2	1
brevis	2	3	1
crystallina	4	5	3
longicornis bispicata	7	5	3
melicerta	4	2	6
melicerta mucicola	8	8	5
melicerta socialis	1	2	2
pedunculata	3	2	0
pilula	3	1	8
tacita	0	1	1
Sinantherina ariprepes	2	1	1
socialis	4	1	1
Stephanoceros fimbriatus	5	2	3
millsii	4	1	6
Utricularia	9	9	10
Myriophyllum	5	2	5
Ceratophyllum	5	9	1
Ranunculus	3	1	2
Chara	2	0	1
Vallisneria	7	0	4
Anacharis	9	7	2
Naias	10	3	4
Fontinalis	10	6	7
Potamogeton	11	13	7
Lemnaceae	4	11	1
Lilies	8	10	9
Gloeotrichia	14	11	8
mean pH	7.6	7.6	6.7
mean bicarbonate (mgm./l.)	28.1	53.7	23.2

Collotheca ornata cornuta occurred most frequently in the central region. This species shows little response to chemical factors and attaches to a wide variety of substrates. But it has, nevertheless, a particular preference for Lemna and Spirodela which accounts in part for the distribution since those plants are by far most frequent and abundant in the central lowland.

Cupelopagis vorax occurred with greatest frequency in the central lowland. Both chemical and substrate conditions are more favorable to this species there than elsewhere.

Ptygura pilula is striking in that it occurred most frequently in the eastern highland where fewest lakes were examined. It has been seen that this species occurs most frequently at low concentrations of bicarbonate and at low pH values. Evidently the distribution is a result of regional chemistry.

Ptygura melicerta mucicola is least common in the eastern highland as is Gloeotrichia. The alga and the rotifer became very abundant only in the hard water lakes of the central region, and both organisms were represented by few specimens in soft water lakes of the eastern and western highlands.

Collotheca gracilipes is completely and *Floscularia janus* almost limited to the western region. There is no explanation evident for these, either in distribution of substrate or in chemical differences.

Regional differences are also evident when the most common species of the fauna are considered. The most common species in the central lowland was *Collotheca ornata cornuta,* but in the western highland, seven other species were more common and five were more common than it in the eastern highland. Lists are given for the ten most common species in all of Connecticut and southern Massachusetts and for the twelve most common species in Wisconsin with the number of localities in which they were found.

Connecticut and Massachusetts:
- *Limnias melicerta* 22
- *Ptygura melicerta mucicola* 21
- *Collotheca ornata cornuta* 20
- *Floscularia conifera* 20
- *Ptygura longicornis bispicata* 15
- *Beauchampia crucigera* 13
- *Ptygura melicerta* 12
- *Ptygura pilula* 12
- *Cupelopagis vorax* 11
- *Floscularia janus* 11

Wisconsin:
- *Ptygura pilula* 30
- *Ptygura beauchampi* 28

Collotheca ornata cornuta 26
Ptygura longicornis bispicata 25
Ptygura melicerta mucicola 21
Limnias melicerta 20
Ptygura crystallina 19
Collotheca campanulata 17
Stephanoceros fimbriatus 17
Beauchampia crucigera 17
Floscularia janus 17
Ptygura melicerta socialis 17

The most abundant species in Wisconsin, *Ptygura pilula,* is tenth from the top of the Connecticut list, although it was the most common one in the eastern highland of Connecticut. *Ptygura beauchampi,* which was very abundant in Wisconsin, does not appear among the ten most abundant Connecticut species. Some of the differences between the two lists may be explained on the relative proportions of hard and soft water lakes in the two sets of collections, but many of them appear to be a result of rather irregular geographical distribution.

GENERAL DISCUSSION

Now that some facts of the distribution of sessile Rotatoria have been traced, it is well to recapitulate the main ideas covered, in connection with existing knowledge of Rotatoria in general. Several aspects of distribution may be considered.

Geographical Distribution

The distribution of most rotifers is geographically extensive, or as it has been put, potentially cosmopolitan. Thus *Testudinella patina, Lepadella patella* and *Cephalodella gibba* are found almost everywhere, and have been recorded from all continents and a number of islands. Actually, however, it is to be doubted that the active distribution results in the deposition of all species in every lake. Methods by which rotifers are distributed most likely include transportation of resting eggs by winds, animals and such agencies as the most usual ones. These agencies are very effective in transporting species over large distances, but can hardly be other than random; thus the actual distribution of rotifer eggs to lakes is irregular. The distribution of common species might be expected to be quite extensive, but "spotty" in that some species have simply never been introduced into certain habitats which may be quite close to ones containing the species. Indeed, of two isolated clumps of one species of plant in a single pond, a species of free-swimming rotifer may be very abundant in one, completely absent in another (Myers, *in litt.*). If collections are adequate to represent actual distribution, then absence of a species from a lake can be the result either of its never having had an opportunity to live there, or of the chemical or physical unsuitability of the water, or even because of biological factors such as the presence of effective predators.

Nevertheless, there is a considerable number of species which seem for no apparent reason, to be restricted to rather limited geographical regions, even though suitable habitats are widely distributed. Several examples can be given. *Kellicottia bostoniensis* has never been found outside of northeastern United States and southern Canada east of the Mississippi, although it is a very common and abundant plankter there, found in the hypolimnia of many rather soft water lakes (Campbell 1941). The species was first found in Massachusetts by the visiting English microscopist Rousselet, who was certainly capable of finding it in England if it lived there. Another species found by Rousselet on the same trip was the planktonic *Ptygura libera* which has been found in several states including New Hampshire and Wisconsin, but never outside of the United States. *Trichocerca platessa* and *Paraploesoma formosum* are large, conspicuous, littoral species found in abundance in many soft, acid water habitats in northeastern United States, but nowhere else although de Beauchamp made a special search for the latter in French habitats similar to those in which it is known to occur (F. J. Myers, *in litt.*) *Acyclus inquietus* is a sessile species always found associated with *Sinantherina,* usually *S. socialis.* It has never been reported outside of eastern North America, although *Sinantherina socialis* is a widespread, common species which has been known in Europe for nearly two centuries. A few species are probably endemic to the Lake Baikal region in Asia. These are distinctive plankters and should have been recognized if they occurred elsewhere. The easily recognizable *Keratella reducta* is known only from South Africa where it may become very abundant. Other examples are given by Ahlstrom (1943). There seem to be no species clearly limited to Europe, although some of the more recently described species, not yet found elsewhere, may be so.

A factor which appears to affect rotifer distribution on a global scale is climate, for there are several species limited to tropics or subtropics, or most common there. Examples are *Lecane papuana* (Edmondson & Hutchinson 1934), *Brachionus falcatus* and *B. mirabilis* (Ahlstrom 1940). On the other hand, *Keratella cochlearis* appears to be much less common in lowland tropics than in temperate regions. In some regions, there seems to be a north-south distribution pattern of species as, for example, European Russia (Dechsbach 1926, summarizing some partially published work by Voronkow).

Obviously, since chemical factors are of importance to some species, it may be expected that to some extent, species distribution will show similarities to regional geological differences which affect water chemistry. This can be seen by examining lists given by Harring & Myers (1922, etc.), Myers (1931, 1936, 1937 and others) and Ahlstrom (1933). In reading the Harring and Myers list for Wisconsin, it should be remembered that habitats from the southern part of the state are included with soft waters of the northeastern highland region. Since many more species are found in acid water, it may be expected that the greater the percentage of hard

waters in a region, the fewer the species that will be found in collections from that region; however, certain species will be found much more frequently, for a considerable number are limited to hard waters.

ENVIRONMENTAL LIMITATIONS

The local fauna of any habitat is apt to depend most on the chemical nature of the water and, for sessile species, to some extent on the flora which also depend somewhat on the same factor. The present work shows that many sessile species are most likely affected by the bicarbonate content, although some react to hydrogen ion also. Harring & Myers (1922) believed that hydrogen ion was the principal factor affecting free-swimming species, deciding that hardness, calcium and magnesium were ineffective.

From data available here, chemical limitation of most sessile species seems to be largely a matter of exclusion from high concentrations of ions other than the hydrogen ion. Species which tolerate high bicarbonate and calcium concentrations are usually found at low concentrations also, while a great many species are not found at high concentrations at all. The most notable exceptions are *Lacinularia flosculosa, Sinantherina socialis* and, to a certain extent, *Ptygura brevis, Stephanoceros fimbriatus* and *Cupelopagis vorax*, all of which are rare in soft waters.

The presence of certain substrate plants is a definite requirement for a few highly selective species, notably *Ptygura melicerta, Collotheca algicola* and *Collotheca gracilipes*. Other species tend to occur more often on certain substrates, although they are not completely limited to one or two kinds. These substrate effects are sometimes facilitated by the flora-chemistry correlations, sometimes opposed. The exact features of plant surfaces which make them good or bad substrates are not known, but probably macroscopic configuration of leaves, minute configuration of the surface, and the physical and chemical condition of the surface all contribute. In general plants with finely divided leaves, as Utricularia and Myriophyllum have larger faunae than those with flat or infrequently branched leaves, as lily pads and Chara. This may have something to do with the surface-volume of ratio and resultant increased productiveness, but can hardly account for the great number of species found on Utricularia as contrasted to such plants as Ceratophyllum, Megalodonta, etc. Certainly, the greater the area of plants in a locality, the larger the rotifer fauna which can develop there. The largest populations of sessile Rotatoria have been found in locations with a quantitatively large flora in relation to volume of water, often in shallow pools carpeted with Sphagnum or masses of Utricularia. The increase of surface area during the growing season must have a tremendous effect on the fauna, both quantitatively and qualitatively.

The various responses to environmental factors result in many species being brought together in lakes more frequently than would happen if their occurrence were quite independent. Both chemistry and substrate preference bring species together in the same sample, as may be seen by examining the frequency of association between species which show either a substrate preference or a chemical limitation. A number of groups of associated species listed on page 38 have certain limitations in common, as for instance, a preference for epiphytes in the list headed by *Collotheca campanulata*. Likewise, of the five species which show the greatest preference for epiphytes (Table 10), each is associated significantly with at least one other, and *Collotheca campanulata* is associated with four. Some of the species which prefer flat surfaces are associated. A strange thing is that the Utricularia fauna has relatively so few associations, although a number of the species are strongly associated with others that have more indifference to substrate. This is likely a result of the abundance and variety of the Utricularia fauna itself. In most collections, when Utricularia was present, almost all rotifer species in the sample were attached to it, while only some of the species were attached to other substrates. Thus the Utricularia fauna is apt to represent, with few exceptions, the entire fauna of a locality, while the fauna of other plants is actually a selected one. The great number of associations observed indicate that localities with a fauna of relatively many species are more common than localities with very few species; more common than if distribution were independent.

Of the 32 species which are limited by chemistry or markedly associated with certain substrates, 15 are correlated with both, 15 with substrate alone, and only 2 with chemistry alone. Of these 32 species, 27 show association with at least one other species. This suggests that substrate is a more powerful factor in bringing species together than the chemistry of water, although it is very difficult to evaluate this in proper terms since correlations between flora and chemistry obscure the picture. A part of the effect may be a result of the sampling process, since it was impossible to examine the entire flora of any locality, but there can be little doubt of its general validity. Competition apparently plays no significant part in affecting species distribution. There is only one case of apparent exclusion, between *Ptygura melicerta* and *Floscularia pedunculata*, and it is probably accidental. Other, less definite examples, can be explained on the basis of chemical or substrate limitation.

LOCAL DISTRIBUTION IN LAKES

Once a species is established in a lake, its local distribution depends mainly on that of suitable substrate and localization of chemical or physical factors to which the rotifer is sensitive. *Collotheca gracilipes* is the best example of a rotifer whose distributions is dependent on a substrate. Chemical variation at any point in the littoral is usually smaller than the tolerance ranges of most species, and it is doubtful if local changes in pH or bicarbonate have a marked effect on the fauna.

We have now considered the larger aspects of distribution, and the distribution in individual local-

ities. This leads to an investigation of the distribution of species on particular substrates and the dynamical relationships of members of populations with each other and with the substrate. Part II of the present series will be devoted to such an investigation.

SUMMARY

1. Many pairs of species of sessile Rotatoria are associated together more frequently than is expected on the hypothesis of random, independent distribution. A few cases of possible mutual exclusion, or replacement are noted. The much greater number of examples of association than of exclusion suggests that while external factors favorable or unfavorable to species are of major importance, competition does not appreciably affect the composition of the fauna.

2. Many species show sensitivity to the chemical nature of the habitat, and occur more frequently in lakes on one side of the median of concentration of certain dissolved materials than on the other side. A discussion of the possible effective factors, out of all correlated variables, leads to the conclusion that some species are very likely excluded from lakes by high bicarbonate concentration, but not necessarily high pH. Examples are *Ptygura melicerta* and *Collotheca algicola* which seem to tolerate high pH but not bicarbonate. *Beauchampia crucigera* and perhaps *Ptygura barbata* are peculiar in that they tolerate neither high nor low pH nor high bicarbonate, and are thus limited to a narrow range of both.

3. The quantitative importance of surface as such in aquatic habitats is demonstrated by showing that larger populations of rotifers are supported by habitats which have more surface area in unit volume.

4. Many substrate plants show sensitivity to the same chemical factors which affect rotifers. This is very evident in the Wisconsin collections, less so in those from New England.

5. Different plants bear different sets of sessile rotifer species. *Utricularia vulgaris americana* has by far the most extensive and varied fauna. In general, plants with finely divided leaves have more rotifer species than those with broad leaves.

6. Some sessile species occur more frequently on certain plants than the commonness of the plants alone would warrant. *Collotheca gracilipes* is almost limited to *Utricularia vulgaris americana*. *Ptygura melicerta* and *Collotheca algicola* occur almost exclusively in colonies of the alga Gloeotrichia, or infrequently, Coleochaete. Several species tend to attach often to epiphytic green algae; for example, *Collotheca campanulata* and *Floscularia janus*. *Cupelopagis vorax* tends to attach most often to broad, flat leaves. *Ptygura brevis*, in the present series of collections, was found almost invariably in forks of finely divided leaves, usually Ceratophyllum. *Ptygura velata* also showed strong reaction to shape of substrate in that it favored to concave, curled tips of *Sphagnum erythrocalyx*. *Ptygura beauchampi* occurred on many substrates, but in any given locality was apt to be highly limited.

7. Experimental analysis of the attachment of *Collotheca gracilipes* shows that under the experimental conditions, it can attach to a number of plants on which it has not been found in nature, but attaches most frequently by far to *Utricularia vulgaris americana*. The observed preponderance of *C. gracilipes* on the young leaves of the plant is shown to be a result of qualitative differences between leaves of different age which seem to be due to the presence in older leaves of a substance which the larvae avoid. The substance apparently is removed by a weak solution of ammonium oxalate and therefore may be a pectin. *Floscularia conifera* commonly attaches to many substrates. In the experiments it also attaches to many, but most often to Utricularia. There is good agreement between field observations and experiment. No reason for the great variety of the Utricularia fauna is evident.

8. The presumed effect of plant succession on the rotifer fauna is discussed. Available evidence suggests that with progressive development of a lake and its flora, the fauna becomes larger in number of species. The presence of *Utricularia vulgaris americana* in any lake has a greater effect on the potential fauna than any other plant. The rootless independence of Utricularia permits it to occur in many types of localities, but by the same token it is limited to quiet habitats; hence, ponds, bogs, shallow bays of lakes.

9. Species of Flosculariidae are about as common in the littoral of large lakes as in small lakes and ponds, while species of Collothecidae are markedly more abundant in small, protected bodies of water. It is suggested that this difference is correlated with a difference in the feeding mechanisms developed in the two families.

10. The rotifer fauna of different regions is shown to be different in the relative commonness of species. This is largely, but not entirely, correlated with chemical differences. Local differences in distribution are largely substrate effects, while direct or indirect effects of chemical differences produce the major regional differences in distribution, but the effect is obscured by random irregularities in original distribution.

REFERENCES

Ahlstrom, E. H. 1933. A quantitative study of the Rotatoria in Terwilliger's pond, Put-in-Bay, Ohio. Ohio State University Bull. **38:** 3-36.

1940. A revision of the rotatorian genera Brachionus and Platyias with descriptions of one new species and two new varieties. Bull. Amer. Mus. Nat. Hist. **77:** 143-184.

1943. A revision of the rotatorian genus Keratella with descriptions of three new species and five new varieties. Bull. Amer. Mus. Nat. Hist. **80:** 411-457.

Beauchamp, P. M. de. 1932. Deux nouveaux cas de phorésie chez les Rotifères. Arch. Zool. Exp. et Gèn. **74:** 385-398.

Brown, C. J. D. 1933. A limnological study of certain freshwater polyzoa with special reference to their statoblasts. Trans. Amer. Micr. Soc. **52:** 271-316.

Burkenroad, M. D. 1939. Quoted by Parr (1939).

Campbell, R. S. 1941. Vertical distribution of plankton rotifera in Douglas Lake, Michigan, with special reference to depression individuality. Ecol. Monogr. **11:** 1-19.

Carl, G. C. 1940. The distribution of some Cladocera and free-living Copepoda in British Columbia. Ecol. Monogr. **10:** 55-110.

Cholnoky, B. V. 1927. Untersuchungen über die Oekologies der Epiphyten. Arch. Hydrobiol. **18:** 661-705.

Coe, W. R. 1932. Season of attachment and rate of growth of sedentary marine organisms at the pier of the Scripps Institution of Oceanography, La Jolla, California. Bull. Scripps Inst. Oceanogr. Tech. Ser. **3:** 37-86.

Coe, W. R., & W. E. Allen. 1937. Growth of sedentary marine organisms on experimental blocks and plates for nine successive years at the pier of the Scripps Institution of Oceanography. Bull. Scripps Inst. Oceanogr. Tech. Ser. **4:** 101-136.

Darby, H. H. 1929. The effect of H-ion concentration on the sequence of protozoan forms. Arch. Protistenk. **65:** 1-37.

Dechsbach, N. K. 1926. Zur Frage über die geographische Verbreitung der Rädertiere in der U. d. S. S. R. und einige Rädertierarbeiten der lezten Jahre. Russ. Hydrobiol. Zeits. **5:** 104-116.

Deevey, E. S. 1938. Typological seccession in Connecticut lakes. Thesis. Yale University.
1940. Limnological studies in Connecticut. V. A contribution to regional limnology. Amer. Journ. Sci. **238:** 717-741.
1942. Studies on Connecticut lake sediments. III. The Biostratonomy of Linsley Pond. Amer. Jour. Sci. **240:** 233-264, 313-338.

Edmondson, W. T. 1938. Three new species of Rotatoria. Trans. Amer. Micr. Soc. **57:** 153-157.
1940. The sessile Rotatoria of Wisconsin. Trans. Amer. Micr. Soc. **59:** 433-459.
1941. Substrate limitations in sessile Rotatoria. Anat. Rec. Suppl. **81:** 109.

Edmondson, W. T., & G. E. Hutchinson. 1934. Report on Rotatoria. Yale North India Expedition. Article 9. Mem. Conn. Acad. **10:** 153-186.

Fassett, N. C. 1930. The plants of some northeastern Wisconsin lakes. Trans. Wisc. Acad. Sci. Arts and Lett. **25:** 157-168.
1940. A manual of aquatic plants. McGraw-Hill, New York. 382 pp.

Frohne, W. C. 1938. Contribution to the knowledge of the limnological role of the higher aquatic plants. Trans. Amer. Micr. Soc. **52:** 256-268.

Gause, G. F. 1936. The Principles of Biocoenology. Quart. Rev. Biol. **11:** 320-336.

Harring, H. K., & F. J. Myers. 1922. The rotifer fauna of Wisconsin. I. Trans. Wisc. Acad. Sci. Arts and Lett. **19:** 553-662.
1928. The rotifer fauna of Wisconsin. IV. Trans. Wisc. Acad. Sci. Arts and Lett. **23:** 667-808.

Hauer, J. 1935. Rotatorien aus dem Schluchseemoor und seiner Umgebung. Verh. Naturwiss. Ver. Karlsruhe. **31:** 47-130.
1937-38. Die Rotatorien von Sumatra, Java und Bali. Arch. f. Hydrobiol. Suppl. **15:** 296-384, 507-602.

Heinis, F. 1910. Systematik und Biologie der moosbewohnenden Rhizopoden, Rotatorien und Tardigraden der Umgebung von Basel. Arch. f. Hydrobiol. **5:** 89-166, 217-256.

Hesse, R., W. C. Alee, & K. P. Schmidt. 1937. Ecological animal geography. John Wiley and Sons, N. Y. 597 pp.

Hicks, L. E. 1932. Ranges of pH tolerance of the Lemnaceae. Ohio Journ. Sci. **32:** 237-244.

Hood, J. 1895. On the Rotifera of the County Mayo. Proc. Roy. Irish Acad. ser. 3. **3:** 664-706.

Hudson, C. T. & P. H. Gosse. 1886. The Rotifera or wheel animalcules. London. 2 vols.

Hutchins, L. W. 1941. The growth and distribution of salt water Bryozoa in relation to salinity. Thesis. Yale University.

Hutchinson, G. E. 1940. A revision of the Corixidae of India and adjacent regions. Mem. Conn. Acad. Arts and Sci. **33:** 339-476.
1941. Ecological aspects of succession in natural populations. Amer. Nat. **75:** 406-418.
1942. The history of a lake. Yale Sci. Mag. **16:** 13 ff.

Hutchinson, G. E., G. E. Pickford, & J. F. W. Schuurman. 1932. A contribution to the hydrobiology of pans and other inland waters of South Africa. Arch. f. Hydrobiol. **24:** 1-154.

Jennings, H. S. 1900. Rotatoria of the United States, with especial reference to those of the Great Lakes. Bull. U. S. Fish. Comm. **19:** 67-104.

Jewell, M. E. 1935. An ecological study of the fresh-water sponges of Northern Wisconsin. Ecol. Monogr. **5:** 461-504.
1939. An ecological study of the fresh-water sponges of Northern Wisconsin. II. The influence of calcium. Ecology **20:** 11-28.

Juday, C., & E. A. Birge. 1930. The highland lake district of northeastern Wisconsin and the Trout Lake Limnologic Laboratory. Trans. Wisc. Acad. Sci. Arts and Le **25:** 338-352.
1933. The transparency, the color and the specific conductance of the lake waters of northeastern Wisconsin. Trans. Wisc. Acad. Sci. Arts and Lett. **28:** 205-259.

Juday, C., E. A. Birge, & V. W. Meloche. 1935. The carbon dioxide and hydrogen ion content of the lake waters of northeastern Wisconsin. Trans. Wisc. Acad. Sci. Arts and Lett. **29:** 1-82.

Keiser, A. 1921. Die sessilen peritrichen Infusorien und Suctorien von Basel und Umgebung. Inaug. Diss. Univ. Basel. Génève.

Kellicott, D. S. 1888. Partial list of Rotifera of the Shiawassee River at Corunna, Michigan. Trans. Amer. Micr. Soc. **10:** 84-96.

Kofoid, C. A. 1908. The plankton of the Illinois River. Part 2. Constituent organisms and their seasonal distribution. Bull. Ill. State Lab. Nat. Hist. **8:** 1-361.

Krecker, F. H. 1939. A comparative study of the animal population of certain submerged equatic plants. Ecology **20:** 553-562.

Lackey, J. B. 1938. A study of some ecological factors affecting the distribution of Protozoa. Ecol. Monogr. **8:** 501-527.

Macan, T. T. 1938. Evolution of aquatic habitats with special reference to the distribution of Corixidae. Journ. Animal Ecol. **7:** 1-19.

Meschkat, A. 1934. Der Bewuchs in den Röhrichten des Plattensees. Arch. f. Hydrobiol. **27:** 436-517.

Meuche, A. 1939. Die Fauna im Algenbuwuchs. Arch. f. Hydrobiol. **34:** 349-520.

Miller, D. E. 1936. A limnological study of Pelmatohydra with special reference to their quantitative and seasonal distribution. Trans. Amer. Micr. Soc. **55:** 123-193.

Morrison, J. P. E. 1932. A report on the Mollusca of the northeastern Wisconsin lake district. Trans. Wisc. Acad. Sci. Arts and Lett. **27:** 359-396.

Myers, F. J. 1931. The distribution of Rotifera on Mount Desert Island. I. Am. Mus. Nov. **494:** 1-12.

1936. Psammolittoral rotifers of Lenape and Union Lakes, New Jersey. Am. Mus. Nov. **830:** 1-22.

1937. Rotifera from the Adirondack Region of New York. Am. Mus. Nov. **903:** 1-17.

1940. New species of Rotatoria from the Pocono Plateau, with a note on distribution. Notulae Naturae. Acad. Nat. Sci. Phila. **51:** 1-12.

1943. Rotatoria of the Pocono Plateau. (In press.)

Noland, L. E. 1925. Factors affecting the distribution of fresh water ciliates. Ecology **6:** 437-452.

Parr, A. E. 1939. Quantitative observations on the pelagic Sargassum vegetation of the western North Atlantic. Bull. Bingham Oceanogr. Coll. **6:** 1-94.

Pearsall, W. H. 1920. The aquatic vegetation of the English lakes. Journ. Ecol. **8:** 163-201.

1921. The development of the vegetation of the English lakes, considered in relation to the general evolution of glacial lakes and rock basins. Proc. Roy. Soc. B. **92:** 259-284.

Pennak, R. W. 1940. Ecology of the microscopic metazoa inhabiting the sandy beaches of some Wisconsin lakes. Ecol. Monogr. **10:** 537-615.

Picken, L. R. 1937. The structure of some protozoan communities. Journ. Ecol. **25:** 368-384.

Pomerat, C. M., & E. R. Reiner. 1942. The influence of surface angle and of light on the attachment of barnacles and other sedentary organisms. Biol. Bull. **82:** 14-25.

Reif, B. B. 1940. Regional plankton studies in Minnesota. Proc. Minn. Acad. Sci. **8:** 19-24.

Remane, A. 1929-1933. Rotatorien. Bronn's Klass. u. Ordn. des Tierreichs. B. IV. Abt. II. Buch 1. Lief. 1-4.

Rickett, H. W. 1922. A quantitative study of the larger aquatic plants of Lake Mendota. Trans. Wisc. Acad. Sci. Arts and Lett. **20:** 501-527.

1924. A quantitative study of the larger aquatic plants of Green Lake, Wisconsin. Trans. Wisc. Acad. Sci. Arts and Lett. **21:** 381-414.

Roll, H. 1939. Zur Terminologie des Periphytons. Arch. f. Hydrobiol. **35:** 59-69.

Rossbach, G. B. 1939. Aquatic Utricularias. Rhodora. **41:** 113-128.

Rousselet, C. F. 1893. On Floscularia pelagica n.sp. and notes on several rotifers. Journ. Roy. Micr. Soc. **1893:** 444-449.

Rudolfs, W., & J. B. Lackey. 1929. The composition of water and mosquito breeding. Am. Journ. Hygiene **9:** 160-180.

Saunders, J. T. 1924. The effect of the hydrogen ion concentration on the behaviour, growth and occurrence of Spirostomum. Proc. Cambr. Philos. Soc. (Biol. Sci.) **1:** 189-203.

Schneider, W. 1937. Freilebende Nematoden der Deutschen Limnologischen Sunda-Expedition nach Sumatra, Java und Bali. Arch. f. Hydrobiol. Supp. **15:** 30-108.

Schumann, F. 1928. Experimentelle Untersuchungen über die Bedetutung einiger Salze, inbesondere des Kohlensauren Kalkes, für Gammariden und ihre Einfluss auf deren Hautungsphysiologie und Lebensmöglichkeit. Zool. Jahrb. Allg. Zool. **44:** 623-704.

Shephard, J. 1899. A new rotifer Lacinularia striolata with a note on L. pedunculata. Proc. Roy. Soc. Vict. **12:** 20-35.

Simpson, G. G., & A. Roe. 1939. Quantitative Zoology. McGraw-Hill. New York. 414 pp.

Skadowsky, S. N. 1923. Hydrophysiologische und hydrobiologische Beobachtungen über die Bedeutung der Reaktion des Mediums für die Süsswasserorganismen. Verh. Int. Ver. theor. u. angew. Limnol. **1:** 341-358.

Snedecor, G. W. 1938. Statistical Methods. Collegiate Press, Ames, Iowa. 388 pp.

Stiller, J. 1940. Beitrag zur Peritrichenfauna des grossen Plöner Sees in Holstein. Arch. f. Hydrobiol. **36:** 263-285.

Surface, F. M. 1906. The formation of new colonies of the rotifer Megalotrocha alboflavicans. Biol. Bull. **11:** 209-219.

Ward, E. B. 1940. A seasonal population study of pond Entomostraca in the Cincinnati region. Amer. Midland Nat. **23:** 635-691.

Wilson, E. B. 1941. The controlled experiment and the four-fold table. Science. **93:** 557-560.

Wilson, L. R. 1935. Lake development and plant succession in Vilas County, Wisconsin. I. The medium hard water lakes. Ecol. Monogr. **5:** 207-247.

1937. A quantitative and ecological study of the larger aquatic plants of Sweeney Lake, Oneida County, Wisconsin. Bull. Torrey Bot. Club **64:** 199-208.

1939. Rooted aquatic plants and their relation to the limnology of fresh-water lakes. In Problems of lake biology (ed. F. R. Moulton). The Science Press. Pp. 107-122.

1941. The larger aquatic vegetation of Trout Lake, Vilas County, Wisconsin. Trans. Wisc. Acad. Sci. Arts and Lett. **33:** 135-146.

Wulfert, K. 1939. Beiträge zur Kenntnis der Rädertierfauna Deutschlands. IV. Arch. f. Hydrobiol. **25:** 563-624.

Yoshimura, S. 1933. Calcium in solution in the lake waters of Japan. Jap. Journ. Geogr. and Geol. **10:** 33-60.

Young, O. W. 1941. A limnological investigation of periphyton in Douglas Lake, Michigan. Thesis, Univ. of Mich. To be published.

ZoBell, C. E. 1936. Periphytic habits of some marine bacteria. Proc. Soc. Exp. Biol. and Med. **35:** 270-273.

1938. The sequence of events in the fouling of submerged surfaces. Official Digest, Fed. Paint and Varnish Production Clubs. 1-8.

ZoBell, C. E., & D. Q. Anderson. 1936. Observations on the multiplication of bacteria in different volumes of stored sea water and the influence of oxygen tension and solid surfaces. Biol. Bull. **71:** 324-342.

MEASUREMENT OF BIRD POPULATIONS

S. Charles Kendeigh
University of Illinois
Champaign, Illinois

Contribution from the Baldwin Bird Research Laboratory, No. 44, and from the Zoological Laboratory of the University of Illinois, Champaign, Illinois.

TABLE OF CONTENTS

	PAGE
INTRODUCTION	69
HISTORICAL DEVELOPMENT	69
TWO MAIN POINTS-OF-VIEW	71
MEASUREMENT OF RELATIVE ABUNDANCE	71
Literature	71
Analysis of new data for northern Ohio	73
Index of abundance	73
Number per hour	74
Measurement of conspicuousness	76
Relative size of wintering populations	77
MEASUREMENT OF ABSOLUTE ABUNDANCE	78
Census methods	78
Census of single or closely related species	79
Literature	79
Bob-white in Ohio	81
Trapping house wrens	82
Local shifts in the population of the house wren	85
The non-breeding population of the house wren	85
Strip census of total populations	86
Literature	86
Reelfoot Lake, Tennessee	87
Census of total populations in sample plots	87
Size of sample plot	87
Nest counts	88
Counting singing males and mapping territories	89
Frequency of surveys	90
Trelease Woods	91
Northern Ohio	93
Computation of population density	94
Recognition and designation of the community	95
Birds of the climax deciduous forest	96
DISCUSSION	99
SUMMARY AND CONCLUSIONS	99
LITERATURE CITED	101
APPENDIX—SCIENTIFIC NAMES OF BIRDS MENTIONED IN THE TEXT	105

MEASUREMENT OF BIRD POPULATIONS

INTRODUCTION

The measurement of the size of animal populations is a popular and important field in ecology and in wildlife management. There has been considerable advance in recent years in methods for the measurement of populations of game animals and to a varying extent in the measurement of populations of other species, including invertebrates, within a community. This particular study deals only with birds and will attempt to summarize and evaluate various methods that have been or are now being employed. The analysis of the avifauna of any region is progressing out of the qualitative phase into a quantitative one, and it would seem that a study of methods to be employed is timely.

Although the compilation of data on size of bird populations in various areas or under different conditions is here of secondary importance to the analysis of methods, considerable data resulting from the writer's own studies will be used to illustrate some of the various techniques and to show their possibilities and limitations.

We wish at this point to acknowledge our indebtedness to the late Dr. S. Prentiss Baldwin, who gave the writer the opportunity for initiating these studies while employed at the Baldwin Bird Research Laboratory at Gates Mills, Ohio. We wish to recognize the aid and numerous records of birds observed in the field furnished by members of the Cleveland Bird Club, especially Dr. J. W. Aldrich, Mr. B. P. Bole, Jr., Mr. B. T. Barnes, Mr. D. C. Kellogg, Miss Margaret E. Morse, Mr. Ralph O'Reilly, Mr. M. B. Skaggs, and Dr. A. B. Williams. We are grateful to Dr. Lawrence E. Hicks for application of one method of analysis to his records of birds observed in the Zanesville, Ohio, region, so that comparisons could be made with the Cleveland region. We acknowledge likewise the comments of Dr. Paul L. Errington, who read the first draft of the manuscript.

HISTORICAL DEVELOPMENT

Previous to the very end of the nineteenth century, quantitative studies were largely limited to indicating whether a species was abundant, common, or rare, and this was based largely on general impressions and the frequency with which the particular observer happened to contact the species in the field. The descriptions of new species and races and the working out of their geographic ranges monopolized the attention of ornithologists and was a necessary preliminary to all other field studies. This approach is still being carried on vigorously in various less well-known portions of the world, but the essential background is now well established in many regions.

This country saw some of the earliest beginnings in the quantitative study of bird populations and still retains much of the leadership in this field. W. L. Dawson (1897) and Lynds Jones (1898, 1901) distinguished between "daily horizons" wherein the numbers of all species seen during a day's outing were recorded, and the "bird census" or the counting of the exact number of individuals on small areas of known size, and through the Wilson Ornithological Club promoted these methods of study. In 1902, Jones urged the taking of a New Year's day horizon, in 1903 he proposed a May day horizon, and in 1904 a July Fourth horizon to be taken simultaneously by as many observers as possible over the country. Such comparative daily lists were published in the Wilson Bulletin until about 1918, when interest in them lapsed.

A similar project was begun by the National Association of Audubon Societies, now the National Audubon Society, in 1900 with the initiation of the Christmas Bird "Census." This project proved to be a popular and ever expanding one and is now as vigorous or more vigorous than ever. It, in essence, is a "daily horizon" taken by many persons over much of North America and adjacent islands during the five days around Christmas. Of similar nature is the statewide "census" during early May recently organized by the Iowa Ornithologists' Union (Grant 1943).

The early work of Forbush in Massachusetts, begun about 1905, undoubtedly exerted an important effect in calling attention to the need and economic value of measuring fluctuations in the abundance of birds from year to year. His estimates as to the relative abundance of birds were based on responses to questionnaires and on reports of numerous observers over the state. This work terminated soon after his death in 1929. The "Season Reports" in the Audubon Magazine follow the same general policy (Griscom 1942) on a country-wide scale.

One of the earliest true censuses of which there is record in this country is a count of 51 pairs of breeding birds on 8 acres made by Alexander Wilson and reported in his American Ornithology in 1811 (Burns 1907). Census work did not begin in earnest, however, until the end of the century. In 1898, Jones marked the location of each bird on a map and determined the number of wintering birds present within a three-quarters mile radius of the center of the city of Oberlin, Ohio. Burns in 1901 reported a breeding bird census of a square mile involving various habitats for the years 1899, 1900, and 1901, and he repeated this census in 1914 for sake of comparisons.

No account of the development of bird censuses can omit the reports of Stephen A. Forbes and Alfred Gross from 1907 to 1923. They developed the strip census method of counting the number of birds in an area of limited width and known length as the

observers traversed through the country. They attempted the measurement of the abundance of birds in various sections of Illinois and obtained figures on number of birds per square mile in habitats of various sorts.

Beginning in 1914, W. W. Cooke (1915) of the U. S. Bureau of Biological Survey (later changed to Fish and Wildlife Service of the United States Department of Interior) urged collaborators over the country to take censuses of breeding birds to give a basis for estimating their economic importance, their influence in the control of weeds, harmful insects, and other undesirable elements in the native fauna, and for determining the adequacy of laws for their protection. These censuses involved the counting of singing males over small areas of known size. The taking of these censuses is still being encouraged, although the project has not been pushed very vigorously in recent years.

The Bureau of Biological Survey began the development of another project in 1920, stimulated by the earlier work of Baldwin (1919), that has had an important influence in measuring and analyzing bird populations, and that is bird-banding. Here the individuals composing the population are identified by numbered bands around their legs so that inter-relations, mortality, and rate of replacement may be followed in detail. The study of individual relations within the population was later improved by developing methods of color-banding, fastening on of colored feathers, etc., so that the individual could be recognized in the field on sight. This has resulted in many detailed studies of population dynamics in individual species (Nice 1941a).

The determination of actual numbers of birds per unit-area is difficult and the degree of accuracy obtained has not seemed worthwhile for some purposes. There have been various "short-cuts" attempted for statistically estimating the abundance of birds in at least a relative manner that have value for comparing different regions or periods of time. Linsdale's (1924) "relative frequency of occurrence" belongs to this category, wherein he gives the various species a ranking determined by the percent of days during an investigation on which each was recorded. "Daily horizons" cannot of course give more than an idea of the relative abundance of the species as likewise can the use of such terms as "common" or "rare." In recent years there have been other methods advanced for getting relative abundance, particularly of game birds.

A great impetus was given the measurement of bird populations by the development during the last dozen years of the field of wildlife management. This was stimulated by the work of Lincoln (1930), Leopold (1931), Errington (1933), and many others for exact measurement, manipulation, and increase of populations of game animals. Contributing influences were doubtlessly the considerable interest and encouragement offered by the federal administration for conservation of all natural resources and the years of drought and hardship that made careful control of game populations necessary to insure their survival and return to a sufficient size to permit normal utilization again for sport. Methods for determination of both absolute and relative numbers of birds were developed, and the field has broadened to include non-game as well as game species.

The yearly breeding bird censuses first organized in 1937 by the National Audubon Society (Hickey, J. J. 1937, Hickey, M. B. 1942) is proving a stimulus for an increasing amount of work in the measurement of total populations, especially of song birds, in various types of communities over the country. At first this project relied largely on contributions from workers around Cleveland, Ohio, who had initiated a series of such population studies beginning in 1932 (Williams 1936).

No attempt will be made to trace the early development of this field of study in other countries although certain parallelisms occur. In the British Commonwealth bird-censusing received a marked impetus from the work of Nicholson (1928) who reported on a complete census of heronries in England. A characteristic of the work in Britain has been this type of census, counting all individuals of single conspicuous species over large areas or throughout the island. The British Trust for Ornithology, centered at Oxford University, has sponsored most of these projects.

The work has not been confined to the British Isles. In Australia, Cleland (1918, 1922) early recognized the desirability of determining actual populations and developed a method of counting birds on strips of known width from which he calculated total number of birds over large districts. In 1937, Chitty & Elton began an ambitious program of following yearly fluctuations in certain species of birds and mammals in Canada. Winterbottom (1936, 1938, 1940, 1942) has analyzed bird populations in northern Rhodesia, and Moreau & Moreau (1931) have worked with populations in Tanganyika.

The measurement of bird population has been a subject of active investigation in Finland. Sundström (1927) and especially Palmgren (1929-1941) and his students and associates have contributed several valuable studies. The usual method employed has been to count all birds on measured strips or areas and with this as a basis to compute the total number of birds in an entire region or province.

In Germany, Schiermann (1930, 1934) made two contributions of merit in determining the bird population over large areas of forests by means of a sampling technique combined with cruising. Zimmerman (1932) made an area census of a marshy habitat. Schüz (1933) surveyed the population of white storks in East Prussia. Hornberger (1939) gives yearly counts of storks from 1931 to 1939.

In Russia, Kashkarov began in 1927 to urge the quantitative measurement and analysis of populations and some few studies have been carried out. This literature is not readily available in this country nor to those unacquainted with the Russian language. Chappellier (1933, 1934) mapped nesting colonies of

the jackdaw in France, but population studies in this country have not been extensive. Aside from the countries mentioned, the study of bird populations in a quantitative manner has greatly lagged, and there are few important contributions.

TWO MAIN POINTS-OF-VIEW

There are two points-of-view or two approaches useful in the determination and analysis of bird abundance. One is simply to get an *index* for each species to permit comparison of relative abundance of different species or of the same species at different times. It is time-saving as usually it is not necessary to locate all the birds as long as the same percent of them is recorded each time. The other is to determine the *actual number* of birds of each species *in an area of known size.* This latter approach also permits comparing the abundance of different species or of the same species at different times. In addition it makes possible a comparison of bird populations with populations of other kinds of animals, such as insects used for food, the numbers of which must be measured by methods not applicable to birds, and makes possible a better evaluation of the ecological and economic importance of species in a community. There are advantages and disadvantages in each approach. The selection of methods to be employed will depend largely upon the intended use of the information and the time and opportunities available.

The determination of relative abundance permits a much larger area to be covered. Ordinarily all that is shown is the frequency with which the various species have been noted by the observer. Often this is all that is desired, but there is no guarantee that this frequency represents the actual numerical relation of the species in the region. Corrections are not ordinarily made for the difference in the conspicuous ness of various species or of the same species at different times; for the difference in behavior between species, as in flocking, extent of home range, etc.; for the amount of time the observer spends in different habitats; nor in the human equation factor, as judgment is required to assign a rank of abundance to each species. To the extent that these corrections are made, the more reliable the data become, but if all the corrections are made as much time and energy will be involved as in the determination of absolute abundance in the first place.

To obtain absolute abundance or the actual bird population, other difficulties are involved. The size of the area censused must be measured and this area must be sufficiently large adequately to sample birds with large home ranges yet not so large that birds with small ranges cannot be counted with accuracy. There is difficulty in finding all the birds in an area, especially when they are not singing. Special methods need often to be employed with different species, and usually repeated trips over the area at intervals of several days are required. During the non-breeding season, birds may shift in and out of the area from day to day. A single observer can usually census only a limited area during any one season. However, the results when obtained are more exact and are useable in a greater variety of ways, so there is a distinct trend in modern ornithological investigation in this direction. Methods used in both points-of-view will be analyzed in the following pages.

MEASUREMENT OF RELATIVE ABUNDANCE

LITERATURE

Fisher (1939) is correct when he explains that species are recorded as "rare" when their actual numbers, usually ones or twos, find their way into the watcher's note-book, "common" when he begins to lose count, and "abundant" when he is bewildered. The observer usually has difficulty in using what data he does accumulate. For instance, if 50 song sparrows were observed during a winter's day in northern Ohio, one would doubtlessly be impressed with their abundance because they occur singly or in small groups and are usually nowhere near that numerous at this season. However if 50 tree sparrows were observed in a single flock during the day one would probably consider them uncommon. Although a flock of birds makes more impression on the observer than a single bird, yet each involves an individual incident of discovery and identification so that several flocks may be required to produce the same impression of abundance as a much smaller number of scattered birds. Since impressions count so much, two competent observers may react differently and give the same species a quite different ranking, hence the unsatisfactory nature of these appellations.

In order to avoid the possible bias and limited experience of a single or of a few individual observers and to cancel out local conditions by covering a large area, questionnaires for compiling the impression of many observers have been used. Forbush (1905) used a questionnaire of this sort to determine whether or not birds had decreased in New England compared with 10, 20, 30, 40 and more years earlier and the approximate extent of this decrease. In his reports as State Ornithologist of Massachusetts he drew upon the experiences of many observers over his area. The same method is now employed in the bimonthly "Season Reports" in the Audubon Magazine covering various sections of the country. Chitty (1937-1942) employs a questionnaire in his Canadian Arctic wildlife inquiry asking his collaborators to give their impression whether a species compared with the year before has increased, decreased, or remained the same. The Fish and Wildlife Service (1941) of the United States Department of Interior uses a similar questionnaire for reports on waterfowl abundance.

Linsdale (1924-1937) has made extensive use of frequency indices to show relative abundance. These frequency indices are computed by dividing the number of days a species is observed by the total number of days observation. The species are then listed in the order of these percentage figures. Likewise,

yearly changes in the frequency index are taken as an indication of change in abundance of a bird. In the use of this method he has been followed by Shaver & Crook (1934), Maynard (1936), Winterbottom (1936, 1940, 1942), Serventy (1938), Rodgers & Sibley (1940) and White (1942). Dice (1930) endorses the use of frequency indices but proposes that instead of days the percentages be based on the percentage of hours or even half-hours of observation in which the species was observed. He himself points out, among other things, that the most important shortcoming of this method is that birds vary in their activity, singing, and conspicuousness at various hours of the day.

There has been some attempt to give the terms—rare, common, abundant—statistical significance. Meylans (1934) designated, as rare, species having less than one pair per square kilometer, uncommon those with about one pair, rather common—2 to 5 pairs, common—6 to 20 pairs, and abundant—more than 20 pairs. Hicks (1937) used ten terms to indicate different degrees of abundance, each based on quantitative data assembled and computed as frequency indices ranging from 0 to 9. Serventy (1938) defines as very abundant those species recorded on 81 to 100 percent of all trips in an area; abundant those recorded on 61 to 80 percent; frequent, 41 to 60; occasional, 21 to 40; scarce, 1 to 20; very rare, below 1. For seasonal species he also worked out percentages of occurrence for the particular periods when they were resident. A breakdown of the percentages into these groups has the advantage of agreeing with units used by plant sociologists (Braun-Blanquet 1932). Lack & Venables (1939) used a complicated method of first indicating each species as 1, 2, or 3 depending on whether 1, 2-9, or over 9 individuals were seen on a particular trip. The scores of each species in all areas were then averaged, the various species ranked in order of their scores, and then each given a new index figure on a percentage basis, considering the most numerous species as 100. White (1942) has designated as abundant those species recorded on 90 to 100 percent of all trips during the breeding season over the same area; common, those recorded on 65 to 89 percent of the trips; moderately common, 31 to 64 percent; uncommon, 10 to 30 percent; and rare, 1 to 9 percent. Although she states that the number of individual birds of one species seen over a period of time parallel the frequency of occurrence of that species, this certainly is not true with colonial nesting species as her own data show. The bank swallow, which on the basis of percentage is designated as moderately common, had a larger number of individual birds recorded during the season than one-half of those species designated as abundant. Recently Stewart (1943) designates six ranks of abundance based on the percentage which the individuals of each species constitute in the total number recorded for all species.

Another approach for indicating relative abundance of different species is the summing of the total number of individuals of each species seen during a period of years regardless of the number of trips taken, as the number of trips taken would be the same for all species provided their migratory status were the same. In this manner, Baldwin, Kendeigh & Franks (1932) determined the relative abundance of hawks and owls in the state of Ohio, drawing upon the lifetime accumulation of trip records of many observers. Eaton (1934, 1936), Seeley (1937), and Chapman (1937) have used the same method.

Speirs (1939) has demonstrated cyclic variations in abundance of some less common but conspicuous species in the Toronto region (Ontario) by simply summing the total number of individuals of each species seen each year without correcting for variations in the number of observers. It is possible to use in the same way the number of birds killed each year, instead of seen, to follow variations in the abundance of game species (Stoner 1934, Middleton 1934). Leopold (1930) showed a decline of snipe in southern Wisconsin, using as his criteria the number killed per trip or the number seen per trip, with some correction of the figures when the trips were very short.

Perkins (1914) and Ganier (1938) have used the Christmas Bird Counts, published in the Audubon Magazine, to show variations in abundance of winter birds, simply by dividing the number of birds seen of each species by the total number of reports. Nichols (1937) varied this procedure, for determining the relative abundance of water-fowl on Long Island, by dividing the total number of birds of each species by the number only of reports listing those species, arguing that if the species were not listed the chances were that the observer did not visit suitable habitats for the species and therefore those lists should not be included. Williams (1918) studied the abundance of the black and turkey vultures by making use of the largest number seen each day.

Bird-trapping data at banding stations have been used to show waves of migration and changes from year to year (DeLury 1934, Braun & Keplinger 1938, Mason 1942). Here the data are similar to those mentioned, except that number trapped per day or season is substituted for number seen. Possible errors lie in the varying effect of weather on trapping, in the lack of uniformity of bait and trapping conditions, and in differences between species, ages, sexes, and individuals in being attracted to the traps.

Some workers believe that the day is too long a unit of time to use and is variable in actual number of hours devoted to observation, likewise the use of the trip as a time unit is questionable as it also varies in length. Grinnell & Storer (1924) list the number of birds seen each hour. They find these numbers are apt to be largest in early morning and next largest in late afternoon. Urner (1930), besides using average number and highest number of individuals of each species per trip at various times of the year, compares the abundance of breeding birds by the number seen per hour. Wynne-Edwards

(1935) compared the abundance of marine birds over five degree zones of longitude across the Atlantic Ocean by use of the mean number seen per hour. For analyzing cycles in the abundance of bob-white, Wing (1937) computed data on the number of hours of observation per bird recorded. Wing & Jenks (1939) mapped the abundance of the downy woodpecker over North America at Christmas time on the basis of number of birds seen per hour in various localities.

Colquhoun (1940) has given careful consideration to various factors involved in getting an accurate estimate of bird abundance. When comparing the total number of adult birds of all species in different areas he walks over a random course at a slow pace and calculates the number observed per hour. However for comparing a single species in different areas he finds a 10-hour basis to be better. When the speed of walking was reduced from 2.3 to 1 mile per hour the number of adult birds observed per hour was reduced proportionately from 1.7 to 1 and the number of species from 1.4 to 1.

Lay (1938) demonstrated a greater abundance of birds on the margin as compared with the interior of forested areas by obtaining counts of birds in time-units of only 30 minutes. All counts were made before 10 A.M. over a winding path.

Although the methods used for determining relative abundance of different species or of the same species at different times by the various workers above mentioned have varied much in detail, in general they follow one or the other of two approaches, *viz.,* frequency of occurrence and number per unit of time. In "frequency of occurrence" there is the assumption that the more abundant species will be more widely dispersed and therefore will be met with more frequently than less abundant species which would be less widely distributed. Although this assumption falls down in case of colonial or flocking species and is not accurate for species that vary in conspicuousness and ease of observation; nevertheless frequency of occurrence does seem to be some approximate measure of uniformity of dispersal for many species. On the other hand, "number of birds per unit of time" gives information on the numerical level of the species in the region, except again for differences in conspicuousness between species, but it furnishes no information as to their dispersal except for the questionable assumption that the more abundant species will be more general in their occurrence. Therefore these two approaches measure two different aspects of abundance as it impresses the observer. Possibly with these thoughts in mind, Hicks & Chapman, in 1933, analyzed 32 years' records of Christmas Bird Counts for Ohio and ranked the species in order of abundance giving equal weight to total number of individuals seen and percentage of all reports listing the species. This was followed by a study of abundance of birds in Muskingam County, using the same method of analysis (Hicks & Dambach 1936). Pierce (1940) made a somewhat similar analysis for northeastern Iowa.

Still another approach to analysis of relative abundance is on the basis of miles covered. Nice (1921-1941), Leopold (1942), and Allan & Sime (1943) have made several reports on number of birds seen from an automobile traveling along country roads. Such counts are especially valuable for the larger and more conspicuous species, such as hawks, and give a substantial basis for comparing abundance of different species or the same species for different regions if such factors are taken into account as speed of travel, character of roadside, weather, time of year, time of day, etc. Nichols (1939) obtained data on the compartive abundance of starlings during two different winters from counts of birds observed from the window of a train. Marples (1935) in England also used observations from a train to determine frequency of birds in agricultural fields of different sorts. Dambach (1941) compared the density of breeding birds in borders of open fields containing various amounts of cover on the basis of number of pairs per mile.

Analysis of New Data for Northern Ohio

An opportunity was afforded the writer when he edited the Bird Calendar, issued quarterly by the Cleveland (Ohio) Bird Club, to analyze the many submitted lists of birds in a quantitative manner and to work out methods of improving the taking of such lists. These lists were made by a large number of both amateur and professional bird students, going at random into all kinds of habitats, spending various lengths of time in each area, and going from one locality to another by automobile or other conveyance. All species were recorded whether seen a few feet away or flying over a distant field so that censuses were not ordinarily taken over any constant area. The number of persons going together in a group varied greatly, and the object was chiefly to see and enjoy as large a number of birds as possible without much thought of exact measurement of populations. If a way could be found to analyze such lists in a reliable statistical manner, this would encourage similar studies of what must now be tens of thousands of such trip lists in the files of ornithologists all over the country. Trip records were available for the Cleveland region beginning in 1933. The Cleveland region was considered as including the area along the south shore of Lake Erie in northern Ohio from Port Clinton, Sandusky, and Norwalk on the west to Chardon and Painesville on the east and extending about 20 miles inland to the south.

Index of abundance. The records were first grouped by months, and the average number of birds of each species seen per trip in each month was computed. Since the trips varied in duration and the birds varied in uniformity of distribution, another computation was made giving the percentage of all trips during the month on which the species was observed. These two figures were multiplied together to give a single figure, but since this figure is a product its square root was extracted to give an index of abundance suitable for comparison. These indices were

calculated for only the more common species of permanent residents, winter visitors, and summer residents, and not for transients.

A sample of the manner in which these indices worked out during two winters is given in Table 1. Five species appear to have markedly decreased in abundance from one winter to the next, three species to have increased, and one species to have remained nearly the same. There may be a question whether these apparent differences in abundance might not be due to a statistical effect. For instance during the winter of 1933-34, the indices are based on 63 reports and in 1934-35 on 90. The trips may not have been of the same average duration during the two years nor may dense woods have been visited in the same proportional number of times.

TABLE 1. Average index of abundance of birds during December, January, and February in denser woods.

Species	1933-34	1934-35
Black-capped Chickadee	23	11
White-breasted Nuthatch	19	12
Tufted Titmouse	18	13
Cardinal	13	9.8
Downy Woodpecker	12	10
Blue Jay	5.3	6.6
Hairy Woodpecker	5.8	5.7
Towhee	3.5	5.8
Pileated Woodpecker	1.4	2.4

To test further the adequacy of this method of analysis, a comparison was made of the abundance of several species of birds in the Zanesville, Ohio, region with their abundance in the Cleveland region during the summer of 1935. The records for the Zanesville region were obtained by Dr. Laurence E. Hicks and his co-workers. Species were grouped according to the habitats or communities in which they occurred and only a general summary is here presented (Table 2). In all instances the indices for the Zanesville region are considerably higher than they are for the Cleveland region.

TABLE 2. Comparison of average indices of abundance of birds in different localities.

Community	Number of Species	Cleveland	Zanesville
Dense woods	30	7.4	20
Open country	51	10.0	58
Marsh	18	4.5	24
Lakes and streams	9	4.1	12

There is no reason to believe that birds are over four times more abundant in Zanesville than in Cleveland, as the figures indicate. Other factors must be involved. Cleveland observers had taken 46 trips during the period, Zanesville observers 37, so this was comparable. Cleveland observers spent only 4.6 hours per trip while Zanesville observers devoted 9.2 hours on an average or exactly twice as much. Nearly twice as many birds should be observed on these longer trips, although the number of species recorded would not be doubled. Zanesville observers covered much more territory by automobile and so were able to sample a larger number of favorable localities. Also important may be the fact that Cleveland observers spent the greatest amount of their time in the woods, while Zanesville observers spent most of their time in open country. Later analyses (p. 76) demonstrated that generally more birds are recorded in open country than in dense woods. For these various reasons the method of computing abundance was abandoned in 1935 for a new method of analysis that was used until the writer relinquished the editorship in 1938.

Number per hour. Doubtlessly the most accurate factor that all observers give in respect to trips is the number of hours spent in the field. It was decided, therefore, to make this the unit of analysis. This accuracy was partly lost when these hours were subdivided, on the basis of information given by each observer for each trip, into the number of hours spent in different major habitats. However this subdivision was necessary as the object of this method of analysis was to present the number of birds of each species seen per hour in its proper habitat. It would not be fair, for instance, to compare the abundance of meadowlark and tufted titmouse on the basis of number seen per hour of total observation if all of the time were spent either in the field or in the woods.

During the four years, 1935 to 1938 inclusive, the average amount of time spent per month by all observers varied for the denser woods from 29 hours in November to 99 hours in May, for the open country from 10 hours in January to 88 hours in May, and for aquatic habitats from 8 hours in August to 48 hours in May. The average number of trips per month varied from 19 in January and August to 73 in May, the number of hours per trip varied from 2.5 in April to 4.3 in July. The average walking speed while looking for birds averaged 1.0 mile per hour for all months with extreme averages of 1.4 miles per hour for December and 0.8 miles per hour for July. Of importance also is that the number of observers per trip varied from 1.6 to 2.1 with a general average of 1.8. There was a nucleus of about eight observers which continued throughout this period of years, while the total number of persons reporting records varied from 14 to 20 per year.

For sake of clarity and brevity the monthly records have been averaged for periods of three months in order to depict average conditions each season and changes from one season to another. Table 3 gives the order of abundance of the different species in the forest. Probably the figures for the winter season are most reliable. At that time leaves are off the trees and visibility is highest. Likewise the birds are less vocal so that difference in loudness of song is of lesser importance in having the species called to the attention of the observer.

TABLE 3. Birds of the forest. Average number observed per hour. Average of years, 1935-1938, inclusive.

Species	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.
Black-capped Chickadee	2.5	1.2	0.4	1.9
Tufted Titmouse	2.1	1.4	0.5	1.3
Cardinal	1.6	2.6	0.5	1.4
White-breasted Nuthatch	1.6	0.8	0.6	1.2
Downy Woodpecker	1.2	0.8	0.3	1.0
Hairy Woodpecker	0.5	0.3	0.3	0.3
Red-breasted Nuthatch	0.5	0	0	1.2
Golden-crowned Kinglet	0.2	1.4	0	3.8
Ruffed Grouse	0.1	0.03	0	0.06
Pileated Woodpecker	0.1	0.2	0.04	0.2
Brown Creeper	0.07	0.3	0	0.2
Red-bellied Woodpecker	0.07	0.09	0	0.07
Barred Owl	0.07	0.06	0.06	0.04

TABLE 4. Yearly changes in abundance of forest birds. Average number of birds observed per hour during the winter season.

Species	1934–35	1935–36	1936–37	1937–38
Black-capped Chickadee	1.8	2.2	2.6	3.0
Tufted Titmouse	2.5	1.8	1.9	2.4
Cardinal	1.6	1.8	1.6	1.6
White-breasted Nuthatch	1.3	1.4	1.5	2.0
Downy Woodpecker	1.5	1.0	0.7	1.4
Hairy Woodpecker	0.6	0.3	0.6	0.5
Red-breasted Nuthatch	0	0.2	0.01	2.0
Golden-crowned Kinglet	0.2	0.2	0.1	0.2
Ruffed Grouse	0.03	0.07	0.18	0.25
Pileated Woodpecker	0.2	0.04	0.1	0.1
Brown Creeper	0.06	0.08	0.04	0.1
Red-bellied Woodpecker	0.01	0.02	0.03	0.2
Barred Owl	0.09	0.08	0.03	0.1

In most species there is a decrease in numbers seen from winter to summer and an increase again in autumn. Part of this decrease is due to migration out of the region, but with permanent residents it is also to be explained by reduced visibility with the leafing out of trees and with reduced singing of the birds when nesting gets well under way. There are some exceptions. The cardinal is shown to be more numerous during the spring than during winter months. Probably this may be explained by their loud singing during the spring months so that more are counted. Golden-crowned kinglets and brown creepers show an increase during the spring on account of large numbers of birds that wintered farther to the south passing through to their breeding grounds farther to the north.

There are local differences in abundance of certain species. The black-capped chickadee ranks at the top of the list in abundance on account of large populations of this species that occur east of Cleveland. West of Cleveland the species is quite uncommon, as Dr. Lynds Jones is able to testify. The red-breasted nuthatch, ruffed grouse, and pileated woodpecker are also more abundant or entirely restricted to the region east of Cleveland.

When average numbers for the winter season are compared from year to year, interesting fluctuations become evident (Table 4). Several species show no consistent tendency either to increase or to decrease. The black-capped chickadee, white-breasted nuthatch, ruffed grouse, and the red-bellied woodpecker show a steady increase in numbers during the four years. The red-breasted nuthatch exhibits a tendency for a marked influx from the north every other winter.

Open country birds, so-called, include species usually found in open woods, shrubby fields, pastures, cultivated farmland, orchards, roadsides, parks, and villages. Some species included in this list, as the blue jay, crow, screech owl, and others, also occur in forests, but they are listed here as the more frequent habitat in which they were observed. The species in Tables 5 and 6 are also listed in the order of their abundance during the winter season.

The starling, English sparrow, and tree sparrow are, according to these figures (Table 5), the most abundant winter birds, but during the spring the robin, starling, crow, and slate-colored junco predominate on account of the influx of migration. The preeminence of the robin is maintained during the summer as many individuals of the other top-ranking species migrate farther north to breed. Perhaps the true rank of the English sparrow is not well established as a few observers could not be persuaded to report numbers of this species seen on their field trips. All species return in large numbers in autumn except the crow. The numbers of this species do not become large in the autumn and winter as nearly all the large concentrations lie farther south.

TABLE 5. Open country birds. Average number observed per hour during years 1935-1938 inclusive.

Species	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.
Starling	18.3	17.8	8.7	50.6
English Sparrow	17.8	7.7	1.4	19.9
Tree Sparrow	14.8	3.7	0	15.7
Slate-colored Junco	8.4	17.4	0	21.6
Horned Lark	5.5	0.8	0	0
Bob-white	3.8	1.8	1.8	2.6
Blue Jay	2.8	1.4	0.4	1.5
Crow	2.3	17.6	1.4	2.7
Song Sparrow	2.1	8.4	3.5	3.7
Cedar Waxwing	1.6	2.7	2.6	0
Goldfinch	1.5	2.0	3.5	3.7
Ring-necked Pheasant	0.7	0.4	0.3	0.7
Mourning Dove	0.3	4.3	2.0	1.1
Sparrow Hawk	0.3	0.4	0.1	1.3
Robin	0.2	19.7	16.6	33.1
Screech Owl	0.09	0.04	0	0.07
Red-headed Woodpecker	0.08	0.2	0.2	0.3
Red-tailed Hawk	0.07	0.1	0	0.1
Red-shouldered Hawk	0.03	0.2	0.1	0

The rapid and consistent decline in numbers of starling and English sparrow during the winters of 1934 to 1937 (Table 6) is astonishing and difficult to explain. Mean temperatures during the four-year period were lowest in 1935-36 and highest in 1936-37. Other species either showed no marked

change in abundance or their fluctuations may have been due to variations in migration.

TABLE 6. Yearly changes in abundance of open country birds. Average number of birds observed per hour during the winter season.

Species	1934–35	1935–36	1936–37	1937–38
Starling	31.9	19.7	12.1	9.3
English Sparrow	....	30.0	19.0	4.3
Tree Sparrow	15.6	23.3	7.5	12.9
Slate-colored Junco	5.1	15.6	3.9	9.2
Horned Lark	17.5	3.1	0.9	0.8
Bob-white	2.7	4.2	4.5	3.6
Blue Jay	3.2	3.8	1.1	3.2
Crow	1.2	4.3	0.9	2.8
Song Sparrow	0.8	2.7	1.6	1.1
Cedar Waxwing	0	1.6	0.3	4.6
Goldfinch	3.1	2.0	0.1	0.9
Ring-necked Pheasant	0.2	1.1	0.8	0.7
Mourning Dove	0.4	0.7	0.2	0.0
Sparrow Hawk	0.3	0.3	0.2	0.4
Robin	0	0.1	0.2	0.7
Screech Owl	0.07	0.2	0.04	0.07
Red-headed Woodpecker	0.07	0.2	0.03	0.06
Red-tailed Hawk	0.08	0.06	0.1	0.02
Red-shouldered Hawk	0	0.08	0.01	0.04

The abundance of water birds during the winter season depends largely on the state of the ice in Lake Erie. When the lake freezes along the shore the birds move farther out to deeper water, migrate, or are restricted to small areas where warm water expelled by industrial concerns keep small pools open. Inspection of Table 7 shows that the scaup duck and the two species of large gulls are the principal wintering lake birds, although there are often large numbers of Bonaparte gulls, a good representation of two species of mergansers, and two other species of ducks. The numbers here given are only of restricted significance. Usually a census was taken by automobile along the lake shore road with stops at localities suspected to have birds wintering. There was very little walking involved so that the numbers are not comparable with those given for open country and forest birds.

TABLE 7. Yearly changes in abundance of water birds. Average number of birds observed per hour during the winter season.

Species	1934–35	1935–36	1936–37	1937–38
Lesser Scaup Duck	47	5	48	36
Herring Gull	17	57	82	21
Ring-billed Gull	14	119	34	15
Bonaparte Gull	6	14	42	54
Black Duck	2.6	14	15	0.8
American Merganser	4.2	8.7	2.5	6.3
Red-breasted Merganser	1.6	3.5	0.3	1.4
Ring-necked Duck	0	0	1.1	0

Table 8 compares the abundance of birds in the forest with open country. At all seasons birds appear to be more numerous in the open country by six or seven times. Very likely birds are more numerous where the habitat is more open and varied and where there is a greater supply of food, cover, and choice of nest-sites, although there is considerable doubt if the ratio in abundance between these two habitats is correct. Birds can be observed at greater distances in the open so that actually a larger area is censused at one time. Likewise the flocking habit is more pronounced among birds of the open country.

TABLE 8. Total number of birds of all species observed per hour.

Habitat	December-February		March-May	
	Number of years	Number of birds	Number of years	Number of birds
Forest	4	11	3	20
Open Country	4	79	3	171

Habitat	June-August		September-November	
	Number of years	Number of birds	Number of years	Number of birds
Forest	2	11	3	32
Open Country	2	68	3	198

When the abundance of birds is compared for different seasons, these figures show birds to be slightly less numerous during the summer than winter but this may be due to their being more scattered and difficult to find. Other information indicates that generally they are more numerous during the breeding season than during winter months. The figures show that birds average two or three times more abundant in the spring than during the winter or summer and also more numerous during the autumn than spring. There are, of course, periods during both spring and autumn migration when birds are temporarily more abundant than these figures indicate. Colquhoun (1941), surveying a forest in England, found 18.0 birds per hour in March, 17.6 in April, 19.0 in May, and 14.6 in June. These figures agree fairly well with those given for the Cleveland region. Urner (1930) found an average of 96 birds per hour in mixed upland habitats during June in New Jersey.

Measurement of conspicuousness. Measurement of bird populations on the basis of number observed per hour permits drawing some general inferences and such measurements are more reliable than the type of indices first utilized. There are inherent inaccuracies and objections that are difficult to eliminate. Some of these have been mentioned. Probably the most important is that species vary in their conspicuousness and in the readiness with which they attract an observer's attention. This is due to differences in size, flight habits, habitat in which observed, flocking tendencies, loudness and frequency of songs and calls, flushing distance, and ease of recognition.

A crow that can be observed a mile away over an open field obviously is not comparable in abundance to a downy woodpecker that may not flush until the observer is within fifty feet.

Colquhoun (1940, 1941) has attempted to measure the relative conspicuousness of English birds during both the breeding and wintering seasons and to correct his bird-counts accordingly. He arrived at a coefficient of conspicuousness by dividing the actual or true number of adult birds present, expressed as number per acre, by the number of adult birds observed per hour. The true or absolute number of birds present was determined by a careful census. The number of birds recorded per hour was on a basis of not less than 10 hours total observation. He also devised means of measuring "song persistence" and "song intensity" as these factors affected the ease with which birds were recorded. Coefficients of conspicuousness computed in this manner are doubtlessly reliable when a true census of stabilized birds can be obtained. The calculation of these coefficients, however, requires considerable research and doubtlessly varies as the activity of the birds varies in respect to migration, singing, nesting, gregariousness, etc.

The writer attempted to obtain indices of conspicuousness for various species by measuring the distance from the observer to the bird at the time that the bird first attracted his attention. This is not the same as the distance at which a species can be identified nor the maximum distance at which a species can be seen. It means rather the average distance at which a species first makes itself known by movement, calling, or simply when remaining stationary. Often when a bird was noticed the observer approached closer to verify his identification or, in case of flocks, to count the total number of individuals. The average of all records as well as the maximum distance at which the bird was first observed are given in Table 9. These figures are for a period from October to March, and to represent more truly the winter season, some unusually long distance records of bob-white, tufted titmouse, and cardinal that were singing or calling are not included.

The average distance a bird is first noticed is considered a better measure of conspicuousness than the maximum distance. The number of records is not adequate for many species to give a true index of conspicuousness, although most species fall in about the order expected. Since this index of conspicuousness is based upon a measurement of distance, this measurement also represents one-half of the width of the strip being censused. The inclusion of some birds beyond this average distance doubtlessly compensates for birds missed at distances less than the average.

Since the number of records for any one species is not large and the differences between species falling near each other in the table are of uncertain significance, the various species are grouped together. For instance, the width of the census strip (twice the average distance at which first observed) for all species from bob-white to golden-crowned kinglet, inclusive, is considered to be 70 feet; from slate-colored junco to downy woodpecker, 150 feet; white-breasted nuthatch to horned lark, 300 feet; robin and starling, 660 feet; and crow, 1,760 feet. Since the average rate of walking during December, January and February average 1.1 miles per hour, the number of acres covered per hour are readily computed. Colquhoun & Morley (1941) arrived at total densities of birds with a very similar method except in order to determine the proper width of the census strip they used the distance at which each species could be identified.

TABLE 9. Distances at which species first attracted the observer's attention, October to March.

Species	Number of records	Average distance, feet	Maximum distance, feet	Area censused per hour, acres
Bob-white	10	19	35	9
Towhee	2	21	30	9
Ruffed Grouse	7	30	50	9
Red-breasted Nuthatch	3	33	50	9
Brown Creeper	2	40	50	9
Golden-crowned Kinglet	10	55	100	9
Slate-colored Junco	17	61	200	20
Barred Owl	2	62	75	20
Song Sparrow	5	66	100	20
Tufted Titmouse	31	67	175	20
Goldfinch	9	69	125	20
English Sparrow	4	75	160	20
Black-capped Chickadee	30	77	150	20
Tree Sparrow	15	78	200	20
Downy Woodpecker	32	89	300	20
White-breasted Nuthatch	35	115	400	40
Cardinal	12	131	300	40
Hairy Woodpecker	17	154	700	40
Blue Jay	15	163	350	40
Cedar Waxwing	2	175	225	40
Horned Lark	2	200	300	40
Robin	8	328	800	88
Starling	9	339	1000	88
Crow	5	880	1300	235

Relative size of wintering populations. Table 10 gives the order and rank of abundance of each species in its own community. To put all species on the same comparable basis, the figures represent in a relative manner the number observed on a hundred acres. This was easily computed as from Tables 3 and 5 the number seen per hour is known and from Table 9 the area effectively censused per hour for each species is given.

Comparing Table 10 with Table 3 for forest birds shows some changes in the order of the species listed according to their abundance, the chief shifts being the higher rankings accorded the downy woodpecker and red-breasted nuthatch. With open country birds, changes in the order of abundance are more startling. The starling which ranked first in Table 5 drops to fifth in abundance leaving the English sparrow the most abundant winter bird. The place of the bob-white in the rankings is raised. It is difficult to believe that there are twice as many bob-white as starlings in this area during the winter, but this may

TABLE 10. Relative abundance of various species during winter months, December to February, 1935 to 1938.

FOREST	
Black-capped Chickadee	12.5
Tufted Titmouse	10.5
Downy Woodpecker	6.0
Red-breasted Nuthatch	5.5
Cardinal	4.0
White-breasted Nuthatch	4.0
Golden-crowned Kinglet	2.2
Hairy Woodpecker	1.2
Ruffed Grouse	1.1
Brown Creeper	0.8
Barred Owl	0.4
OPEN COUNTRY	
English Sparrow	89.0
Tree Sparrow	74.0
Slate-colored Junco	42.0
Bob-white	42.0
Starling	20.9
Horned Lark	13.8
Song Sparrow	10.5
Goldfinch	7.5
Blue Jay	7.0
Cedar Waxwing	4.0
Crow	1.0

nevertheless be true. The bob-white seems less numerous because it is difficult to flush, while the starling occurs in flocks which are especially conspicuous in cities or near human habitations.

Since the relative position of the various species is determined by estimating the number seen per 100 acres, this would seem to indicate also their absolute abundance, a true strip census. This, however, does not necessarily follow. The total sum of relative values of forest birds is 48 and open country birds is 312. When these values are compared with results obtained from censusing birds during the winter time by other methods (pp. 93-94), the sum of relative values for forest birds agrees fairly closely with the number of individuals determined per 100 acres by the census method, but the sum of relative values for open country birds is several times higher. Doubtlessly this may be explained by the difference in the nature of the two communities. The forest community is more nearly uniform in nature except for occasional thickets and ravines. Probably a strip count through a forest would more accurately sample the bird population because all portions of this area are nearly alike and individual birds or bird groups would be fairly uniformly spaced. Therefore, the figures for relative abundance of forest birds may represent their actual numbers per 100 acres and be a true census. In the open country, however, birds are concentrated in forest-edges, shrubby or weedy fields, fence rows, refuse centers, etc., and are absent from open fields where vegetation is scant. The usual bird observer is after a long list of species and naturally traverses those areas which he knows from previous experience are likely to be areas of concentration and avoids those areas where birds are less likely to occur. Therefore our relative values for ranking the species of open country birds are without significance for indicating absolute abundance. In spite of these difficulties, the reasoning demonstrates that for ultimate reliable determination of the relative abundance of birds, analysis must be so complete as to put the results on essentially the basis of a true census. For the vast number of trip records compiled by bird students in the past, it is very doubtful if the necessary information is available in sufficient detail to make such analysis possible. It appears that ornithology must start almost, but not quite, anew and gather exact quantitative data on the abundance of birds by the development of improved census methods.

MEASUREMENT OF ABSOLUTE ABUNDANCE

CENSUS METHODS

A comparison and description of various methods for taking bird censuses have been outlined by Kashkarov (1927), Nicholson (1931), Hosley *et al* (1936), Lack (1937), Bray (1938), Wight (1939), James Fisher (1939), and Palmgren (1941). Lack (1937) and Hickey (1943) have compiled census data for many areas. These methods may be conveniently grouped as to whether they apply to the counting of birds over a strip area of known width and length or on a plot of usually some other shape. Both involve direct enumeration of the birds, their nests, or other evidences of their presence. A fundamental difference is that over the strip area or belt transect a census is taken but once, a larger and greater diversified area may be covered, the desirable width of the area needs to be established, and the final results are usually not so dependable. This may be called the *strip census.*

A census over a permanently established area may be designated, for contrast, a *plot census.* A plot may vary in size from a few acres to an entire continent. The plot often includes several communities or habitats, but for most effective use as a sample count capable of application elsewhere it should contain but a single major type of community. Different methods may be employed to count individuals of different species; likewise, repeated visits permit censusing each species at the most favorable time. Plot censuses when properly carried out furnish data of greatest accuracy.

For both types of census, the number of birds become known over areas of known size. Density can then be computed in terms of number per unit-area. Lack (1937) urges this expression in terms of number per 100 acres (40 hectares), and this is the standard adopted by the National Audubon Society in their breeding bird censuses. This standard is simple, clear, avoids fractions, and is easily reducible to birds per acre if this is desired. During non-breeding seasons birds of both sexes and all ages are usually counted by direct observation and the density expressed simply as number of birds per 100 acres. During the breeding season it is desirable, where possible, to know the number of adult

birds of each sex that are actually breeding and also the number of birds present but non-breeding. Usually the density during the breeding season is expressed as number of pairs per 100 acres. Davis (1942) has recently suggested that the unit should be one of volume of vegetation (100,000 cubic meters) to compensate for variations in the number of birds due to differences in height and density of the vegetation, viz., prairie, shrubby fields, forest, etc. However, correlation of bird population densities with the amount of vegetation in an area is only one way in which such data may be utilized and retaining the density figures on the simple areal basis will permit studies of many other sorts.

Both the strip census and plot census may be concerned with a single species or with the total population of all species. Since the count of total populations is usually more difficult and complex, census methods applicable to single species or groups of closely related species will be first considered.

CENSUS OF SINGLE OR CLOSELY RELATED SPECIES

Literature. The census of waterfowl over the North American continent is one of great importance in their management and in the formation of hunting regulations, yet the censusing of waterfowl presents problems of special difficulty.

In censusing water birds in sanctuaries on the Gulf of St. Lawrence, Lewis (1931, 1942) used actual counts of birds present, their nests, as well as estimates. In computing the number of ducks in the Illinois River valley, Hawkins & Bellrose (1939) count as well as they can from shore and boat the number of birds on several lakes, get the area of these lakes by using planimeters on large scale maps, compute the number per acre on three classes of lakes of different attractive value to the birds, classify all the lakes as to their attractiveness, then on this basis compute the number for the entire valley both before and during the hunting season. The final results, however, are only rough estimates, and during recent years they have censused about three-fourths of all the lakes by direct counts. More Game Birds in America (1935) arrived at an estimate as to the number of ducks in North America by using several different methods on various sample areas. Direct counts of birds were made on small accessible ponds and lakes. In large marshes floating blinds were used. On the extensive less accessible breeding grounds of western Canada observers used cabin airplanes, either counting or estimating the numbers directly seen or photographing the lake and then making the counts from the developed prints. All counts and estimates were made during the summer. Mason (1936) also reports the use of airplanes in making surveys of waterfowl in Florida.

The Fish and Wildlife Service of the United States Department of Interior (1941) send special investigators into the principal breeding and wintering grounds of the ducks. These investigators inspect many areas personally and receive reports from local observers. In January each year a special survey is organized that involves dozens of observers over the country who personally count or estimate the number of birds on the important wintering areas within a period of a few days to avoid error due to birds shifting from one area to another. Instructions are given for use of airplanes in making these surveys. When reports are compiled there is an approximation of the total number of birds over an immense area.

In a sense, these studies with waterfowl are not true censuses, as estimates rather than actual counts are always involved where large aggregations occur. A common method of estimating is to count a group of individuals up to 100, then visually block off additional groups of a hundred birds comparable to the first count until 1,000 birds are reached, then similarly block off groups of 1,000 until the entire aggregation is covered. When the birds are actively feeding or diving, allowance is made for birds out of sight. Where the birds leave the marshes in the evening to feed in upland fields, their numbers can often be closely estimated as they pass over in long flight lines. If the total area covered by a resting flock of waterfowl can be estimated, a figure for the size of the flock may be obtained by allowing one bird for each square yard and then deducting one-third of this number for open spaces (Bell 1937).

Lincoln (1930) has worked out an interesting method that furnishes a short-cut for estimating in a rough manner the total number of ducks in North America. Each year several thousand ducks are banded and released. These are exposed to mortality from hunters to the same extent as are unbanded birds. Hunters that kill banded birds report these bands to the Fish and Wildlife Service. If the total number of birds killed each year is known, then the number of banded birds killed should be the same percentage of the total number killed as the total number banded is to the total number of ducks in existence at the beginning of the hunting season. Lincoln has found that this percentage ratio is usually around 12. The method is subject to error when banded birds are not reported, but this is offset by doubtlessly many birds being killed and not reported. Likewise the method is not reliable for small areas or for small samples of the total population. Winkler (1930) proposed a similar method for taking censuses of land birds in Europe, that involved percentage of banded birds in total number of birds coming to banding stations. There may be inaccuracy involved here in that birds once caught and banded may not return to the traps as readily as new birds, although some individuals acquire the trap habit and return even more frequently.

There have been many censuses of single species or small groups of species over extensive areas in Europe. Schüz (1933) surveyed the population of white storks in East Prussia, and gave the number of birds per square kilometer of the area in general and also per square kilometer of suitable habitat.

Nicholson (1928) first reported a census of nearly all known British heronies in 1928. In later years the census covered a few selected heronies to serve as an index of yearly fluctuations (Alexander 1942).

Morrey & Lockley (1933) and later Wynne-Edwards, Lockley, & Salmon (1936) took censuses of gannets on islands through use of photographs. Vevers & Fisher (1938) censused gannets by direct counts and they also developed a new method. This involved the determination of the ratio between the number of birds alighting on the side of the cliff per unit of time and the actual number of nests or pairs there. When this ratio was established, extensive areas could be covered more quickly by simply counting the number of birds alighting during the time unit adopted. This method was used in several later studies. In 1939, Fisher & Vevers give a figure for the breeding population of the gannet over the entire world. In another extensive study Fisher & Waterston (1941) give data on the breeding population of fulmars in all known localities.

Hollom (1933, 1936) and Harrisson & Hollom (1933) organized a series of censuses of the great crested grebe which required the cooperation of many observers over England, Scotland, and Wales. Hollom (1940) has also surveyed colonies of the black-headed gull. Harrisson & Hurrell (1933) censused the black-backed gull in England and Wales; Lister (1939) has a report on the lapwing. Goddard (1935) studied short-eared owls in a small tract, and Middleton (1934-1937) concentrated on populations of partridges in Great Britain.

Among passerine species, there have been several counts of rooks in various sections of England (Roebuck 1933, Yapp 1934, Tucker 1935; Cramp & Ward 1936, Mitchell 1938). Boyd (1933-1936) and Cramp & Ward (1934) have reported a series of studies with swallows, Marples (1934) has a population report on starlings, Price (1935) has two separate reports on nightingales, chiff-chaffs, and willow warblers, and Serle & Bryson (1935) have one on the dipper. Most of these studies deal with conspicuous species or those the nests of which are easily found or that occur in large colonies or roosts or that are especially sought after by sportsmen.

Returning to work done in this country, many population studies over large areas deal with game species, especially upland game. Leopold (1931) made a general survey of the north-central states. Later Bennitt & Nagel (1937) made an extensive survey of Missouri. For bob-white and pheasant populations, counts were made on selected farms with the help of dogs, many hunters' reports were utilized, and kill records were obtained.

Errington & Hamerstrom (1936) used various techniques in their winter censuses of bob-white over unit areas varying from one to five square miles. These included counts of birds through use of dogs, from tracks in the snow, from body impressions made in the snow or dirt at roosting places, and in flushed coveys. They found their counts became less accurate when the population went beyond 1 bird per 4 acres. Trained bird dogs are of great aid in increasing the accuracy of game bird censuses (Wight 1931, 1934). In late summer, however, they cannot be as effectively used, except in early morning hours, as the abundance of pollen and high temperatures greatly decrease their efficiency (Bennett & Hendrickson 1938a). Allen (1938) and Lay (1940) used long lines of men and dogs to traverse an area and to obtain complete counts of bob-white and pheasants. A line of 20-40 men could census 600 to 1,200 acres in 6 hours. In open country the men were placed 12 yards apart but in dense brush this space was decreased to 6 yards.

Since valley quail do not commonly "freeze" when alarmed, the use of pointer dogs for censusing is less successful with this species. Glading (1941) describes an effective method wherein three men rode on horseback about 200 feet apart with each man counting birds that flushed within 100 feet on each side of him. At the edge of the area the three men rotated and returned on the next adjacent strip, the outside man always riding slightly ahead to prevent flushed coveys from spreading into uncensused areas and being recounted. Under good weather conditions and in brushland where the cover was not too dense, 750 acres could be covered in an eight-hour day with an accuracy of 90 per cent.

R. T. King has worked out a method for censusing ruffed grouse that seems to be effective. The area to be censused is laid off into 40 acre blocks by compass lines which the observer follows. It is necessary not only to count all birds flushed but also to get the average distance from the observer at which they flush. Twice the average flushing distance is taken as the width of the census strip, this multiplied by the distance traveled gives the area censused. When the total area is divided by the area censused and multiplied by the number of birds observed, it gives the population over the entire area. L. W. Fisher (1939), using this method, found the average flushing distance to be about 45 feet and he used an average width of about 87 feet for the census strip. If the average flushing distance were once found to be constant for certain types of cover or seasons, it would not be necessary to redeterminate it for each census strip. In censusing Canada geese in the Bear River Migratory Waterfowl Refuge, Williams & Marshall (1937) found they could count geese on their nests in spring before the vegetation had attained full growth in a strip 200 yards on each side of a small boat.

Bennett & Hendrickson (1938) devised a short-cut method for censusing ring-necked pheasants in Iowa. By comparisons between known populations in an area and the number that could be seen from an automobile, they found that 8-10 birds recorded to a mile, while traveling at 20 miles per hour along country gravel roads between 6 and 8 A.M., indicated a population of 1 bird per 4-5 acres, 2 birds per mile indicated 1 bird per 7-9 acres, and 1 bird per mile indicated 1 bird per 18 acres. Randall & Bennett (1939) revised the index values for Pennsylvania

as follows: 6-8 birds a mile indicated a population of 1 bird per 2 acres, 2-3 birds a mile indicated 1 bird per 4 acres, 0.7-1.8 birds a mile indicated 1 bird per 6-7 acres, and 0.25 to 0.60 bird per mile indicated 1 bird per 18-20 acres. The principle involved is that the birds roost at night in open fields and do not seek heavy cover or cornfields until the morning dew has evaporated.

Allen (1942) found that when the total kill of cock pheasants in an area is known the total population of the species may be estimated from the change in sex ratio after the hunting season compared to what it was before the season opened. The number killed is equal to the percentage drop in ratio of males to females.

Davison (1940), Lehmann (1941), and Douglass (1942), in censusing prairie chickens, counted from a car or blind during early spring mornings the number of males on the various courting grounds over the area. Inaccuracies in the method appeared to be due to changes in the weather and to the difficulty of distinguishing the sexes. Davison states that with this method 16 square miles could be censused in 5 or 6 days. Lehmann also used other methods. He found that 2,000 acres of open prairie could be accurately censused in a day by pulling an inch rope, 60-120 yards long, between automobiles traveling 5-15 miles per hour. He tells how early settlers and market hunters in Kansas and Texas used to hunt these birds by pulling ropes between wagons spaced 300 yards apart.

Graham (1940) has successfully used a method for censusing ruffed grouse and other birds with loud calls, whereby observers are stationed before 6 A.M. at various locations around a quarter section. Each observer records the direction, relative distance, and time at which the birds drum or call. When plotted on a map the intersection of two lines gives the location of the bird within 300 feet.

Moffitt (1943) has conducted annual censuses since 1931 of black brant wintering off California. Direct counts are made of bird concentrations with binoculars either from boats or from points of advantage along the shore. Allen (1937) made a census of all the heronies on Long Island. Watson (1907) and Wright (1913) obtained figures for total populations of terns and cormorants nesting on islands by finding the total area covered by the colonies and multiplying this area in square feet by the average number of nests per square foot.

Population studies of the crow over large areas in the winter have been given special attention as the birds are then concentrated in large conspicuous roosts whose size may be estimated. Emlen has conducted such counts for New York (1938) and California (1940), and Black (manuscript) for Illinois.

McClure (1939, 1942) censused mourning doves in Iowa from April to September by counting the number of males cooing within 100 yards of the observer either before 9 A.M. or after 5 P.M. This gave the number of birds over an area with a diameter of 200 yards. He states that only breeding birds coo and he has worked out correction figures for time of day, temperature, weather, wind, and season. When a census of nests is made, he has a ratio by means of which the total production of young for the season may be computed. In a recent review (Wils. Bull. 55, 1943: 198-200), Nice has pointed out certain fallacies in his methods.

Bob-white in Ohio. In 1933, Kendeigh presented data on yearly bob-white populations in Ohio for the period 1908 to 1931, inclusive. Since another 11 years have elapsed the curve showing abundance (Figure 1) may be extended. These data give an estimate of the total number of bob-white in the state in early winter based on an analysis of the Christmas Bird Counts of the Audubon Magazine. The number of these counts in Ohio have varied from 11 to 20 during the last 11 years. Although fairly well scattered over the state, the number of sample counts is too few and the conditions of observation are too variable and uncontrolled for permitting great confidence in the results as a true census, but since many localities are represented year after year the data give an indication of at least major yearly changes. During these 35 years the toal population has varied from less than 1,000,000 to over 4,000,000 birds. Since about 1920, the population has varied around 3,000,000 birds or approximately one bird per 9 acres (11 birds per 100 acres). Although this figure seems a reasonable one for the population of an entire state and closely approximates the estimate made by Bennitt & Nagel (1937) for the median number of birds in the entire state of Missouri in the early fall of 1934, it needs verification from a larger series of direct counts in properly selected sample areas.

In arriving at the figure for the population of birds during any year, the Christmas Bird Counts were first tabulated under the following headings: number of parties in the field at each locality, number of observers at each locality, combined hours in field for all parties, total mileage on foot for all parties, amount of snow on ground, and number of bob-white observed. From this table, the average number of observers per party for all localities was determined as well as the average number of miles covered per party. To determine the area that was censused it was assumed that each observer was responsible for a strip 75 feet wide which would allow an average flushing distance for the birds of 37.5 feet. This was then multiplied by the average number of miles covered per hour per party and by the total number of parties. To allow for increased efficiency in censusing, this area was multiplied by the average number of observers in the party. Two persons will doubtlessly find more birds than will one, when going over the same route, because of the greater disturbing effect that they have, the increased noise that they make, and by their going along opposite sides of hedges, thickets, etc., although probably they will not find twice as many nor will three persons find three times as many birds. Not knowing the absolute value of this efficiency factor there may

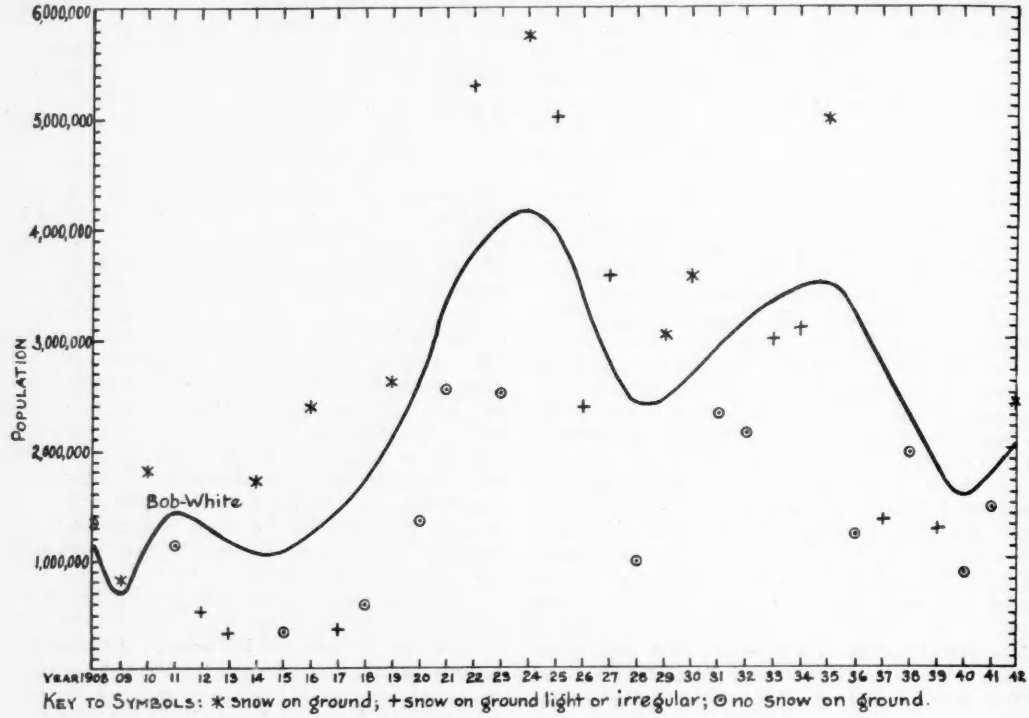

FIG. 1. Trend of yearly fluctuations in size of populations of bob-white in Ohio.

be some inaccuracy in this step of the computation; however, the exaggerated size of the area considered censused may compensate somewhat for the tendency of observers to select forest-edges, field borders, and similar situations where the birds are more abundant and to avoid open fields and other areas where birds are usually absent. The next step was to determine the number of birds observed per hour by all parties. When the area in square miles covered by all parties per hour was known, the number of birds per square mile was readily computed, and then this figure was multiplied by the number of square miles in the state as a whole.

This figure needed one more important correction based on the amount of snow on the ground. When there was a good snow cover birds were more easily located by their tracks, so that population figures for those years are higher proportionately than for years with little or no snow. In Figure 1 the calculated number of birds for each year is plotted and surrounded by a symbol indicating the amount of snow present. The final curve showing the general trend of variations in the size of the population from year to year was drawn by eye roughly midway between years with good snow cover and years with none. This curve does not exactly duplicate the one given by Kendeigh (1933) in that the small peak for 1916 given in that paper was due to an error in plotting the data.

There is still a difference of opinion among students of the bob-white as to whether the species is cyclic in numbers, irruptive, or relatively constant. Perhaps there will be differences between regions (compare with Errington 1941), but for Ohio this curve strongly suggests variations of a rhythmical or cyclical nature with former peaks in 1911 or 1912, 1923 or 1924, and about 1935, with low points about 1909 (?), 1915, 1928 or 1929, and 1940. Eliminating the doubtful low year of 1909, these points in the curve come at intervals of 12 or 13 years.

Trapping house wrens. Trapping and identifying individual birds at or near their nests is a practicable method for measuring and studying small populations in limited areas. Nice (1930) has done this for the song sparrow simply by placing a trap on the ground within the bird's territory near its nest. Trapping and individual identification of adult birds have been the means for working out several excellent studies on the dynamics of populations and on the interrelations of individuals within a species, especially in respect to territory and mating (Nice 1941a).

Practically all nesting house wrens on Hillcrest Farm (Baldwin Bird Research Laboratory) were captured at their box-nests by trap-perches and identified by numbered government bands for the period from 1915 to 1939 inclusive. In addition the population for 1940 was estimated from the

number of broods (three) known to have nested. During 1940, the number of boxes and other environmental conditions remained similar to 1939, and the census of nesting boxes was made by a person who had lived on the estate for several years and was familiar with the work.

When the total number of adult house wrens of both sexes is graphed (Figure 2) a distinctly fluctuating curve results. For all years previous to 1921 the record is not too clear, but except for 1916, the available evidence indicates that the entire population was identified or very nearly so. Beginning with 1921 this was more certainly true. Beginning with this year also it is fairly certain that the number of boxes available was always ample and more than were occupied at any one time. Probably this was true for earlier years. In the records for 1917 one box had the number of "51," and there is every reason to believe the boxes were numbered consecutively as they were erected. Except for a slight drop in 1917, Figure 2 shows a steady increase in the size of the population up to 1922. Although there are few notes for these early years, all the information available indicates that there were practically as many boxes available in 1917 and probably also in 1915 as there were in 1922, so that this increasing population was not due to an increasing number of nest-sites. There is no record of whether boxes were available before 1915, although in 1921, Dr. Baldwin (p. 238) wrote, "It was in the spring of 1915 that I began the use of trap nest boxes. . . ." The inference from this statement is that boxes without arrangements for trapping the adults may have been present during earlier years.

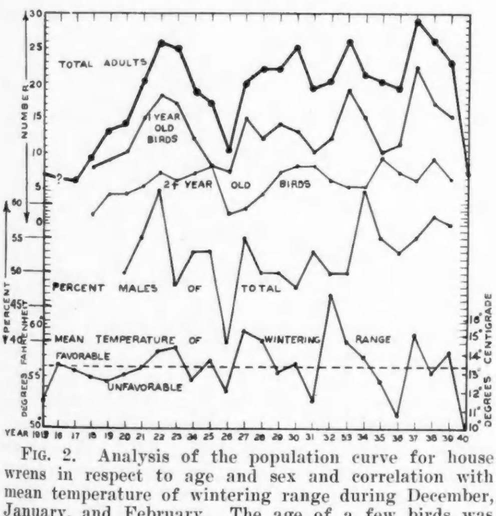

FIG. 2. Analysis of the population curve for house wrens in respect to age and sex and correlation with mean temperature of wintering range during December, January, and February. The age of a few birds was not determined.

It is possible to consider the climb in size of population to 1922 as representing a natural growth of a population when an area becomes available for colonization, as old birds returned and new birds discovered the area. However eight years, from 1915 to 1922 inclusive, constitute too long a time to suppose that the increase was due just to the slowness of colonization. From 1915 to 1919 the population increased only from 7 to 13 birds. From 1919 to 1922 the increase was from 13 to 26 birds or at a much accelerated rate and similar to the rise that occurred from 1926 to 1930. It seems logical to suppose that the years from 1915 to 1919 were unfavorable for establishing a large population. The drop in population in 1926 and in 1940 needs also to be explained. If 1917 is taken as a low year, then the periods between successive very low populations are 9 years and 14 years.

Superimposed on these major fluctuations in population is possibly a smaller variation of 3-4 years. Beginning with a peak in 1922 another peak was due in 1926 but was thwarted by the great dip in population that will presently be explained. The secondary cycle began again in 1930, and is represented by peaks in 1933 and in 1937, but was interrupted again by the great drop in 1940. This smaller superimposed cycle cannot be considered substantiated in this record because the record covers too small a period. Although these data on breeding populations over a period of 26 years is one of the longest on record for any passerine bird, it should cover probably a century to furnish sufficient evidence. Long term studies of animal populations, preferably in undisturbed natural areas, should be initiated even now and conducted by institutions, as universities and museums, where the continuity can be insured beyond the lifetime of any single investigator.

When the population of a species is identified as individuals, analysis of variations in the population in respect to age and sex is possible. This was done for the house wren for the years 1918 to 1939 inclusive (Table 11). All unbanded birds appearing each year were considered as birds in their first breeding season, or approximately one year old (Kendeigh & Baldwin 1937). Tables 12 and 13 show further what can be done in analyzing a population in respect to its reproductive activities when the identitfy of the constituent individuals is known. All three tables were compiled after the territorial and mating relations had been carefully analyzed (Kendeigh 1941a). As there were some unidentified birds and incomplete nesting attempts the data here presented differ in several cases from those given in our earlier paper (Kendeigh & Baldwin 1937). Some birds, the stay of which was only temporary are here included although omitted in the earlier table, and some corrections are made as the analysis of territory behavior permitted more definite recognition of individuals that were not banded. Probably the figures given in the present paper represent a better index of the yearly population, although the fundamental conclusions of the earlier paper are not changed.

Figure 2 is an attempt to analyze the population curve of the house wren and to determine its various components. Considering first the age factor, it is

TABLE 11. Analysis of yearly populations of house wrens in respect to age and sex.

Year	Number of identified birds in each age class						Total identified	Per cent males	Total population
	1 yr.	2 yr.	3 yr.	4 yr.	5 yr.	6 yr.			
1915.....	..	..	..	..	..	..	..	..	7
1916.....	2	1	0	0	0	0	3	..	3?
1917.....	6	0	0	0	0	0	6	..	6
1918.....	8	1	0	0	0	0	9	..	9
1919.....	9	3	1	0	0	0	13	..	13
1920.....	10	4	0	0	0	0	14	50	14
1921.....	15	2	3	0	0	0	20	55	20
1922.....	18	4	0	3	0	0	25	62	26
1923.....	17	5	1	0	0	0	23	48	25
1924.....	12	5	2	0	0	0	19	53	19
1925.....	8	2	5	1	0	0	16	53	17
1926.....	7	0	0	1	0	0	8	40	10
1927.....	15	2	0	0	0	0	17	55	20
1928.....	12	4	0	0	0	0	16	50	22
1929.....	14	4	3	0	0	0	21	50	22
1930.....	13	4	2	2	0	0	21	48	25
1931.....	10	6	1	1	0	0	18	53	19
1932.....	12	2	3	0	1	0	18	50	20
1933.....	19	4	0	1	0	0	24	50	26
1934.....	15	3	2	0	0	0	20	62	21
1935.....	10	7	1	1	0	0	19	55	20
1936.....	11	2	3	1	1	0	18	53	19
1937.....	22	2	1	2	0	1	28	55	29
1938.....	17	6	2	1	0	0	26	58	26
1939.....	15	4	2	0	0	0	21	57	23
1940.....	..	..	..	..	..	..	..	..	6
Total 1916-39	297	77	32	14	2	1	423	53 *ave.*	18 *ave.*
Per cent.	70	18	8	3	0.5	0.2	..	..	..

apparent that the curve for number of one-year-old birds that were breeding for the first time agrees very well with the curve for the total population. On the other hand, the curve for variations in number of older birds that were present for the second or later years shows no such close correlation. From 1918 to 1925 there was a gradual increase in the population of older birds, but the peak in the total population during 1922 and 1923 was due to first-year breeders. This youngest age class already had begun to decrease in numbers in 1924 and this continued in 1925. During 1924 and 1925 the two-year and older adults increased slightly to compensate in part for the reduced number of one-year-olds. In 1926, the pronounced drop in the total population curve was due to these older birds abruptly falling off in numbers while the one-year-olds decreased only slightly.

In 1927, one-year-olds quickly recovered to a moderate abundance which they more or less maintained until 1930. The number of two-year-olds increased steadily to 1930. The trough of 1931 was due to a drop in number of one-year-olds and not the two-year-olds. This latter age group fluctuated back and forth until 1939 and the two peaks (1933, 1937) and one trough (1936) in the total population curve was due primarily to variations in the number of one-year-olds. The great drop in 1940, however, included both age groups.

This analysis indicates that variations in the yearly abundance of the species are due principally to variations in the number of young birds to reach sexual maturity and return to the area each year. This, in turn, may have been due to variations in the amount of reproduction the preceding year but it more likely caused by variations in mortality over winter (Kendeigh & Baldwin 1937). Unfavorable climatic conditions occasionally occur, and to them young birds appear more sensitive and responsive than older birds.

When the sex ratio is expressed as percentage males in the total population and plotted (Figure 2), there appears some tendency for a positive correlation with the curve of total abundance during the first half of the total period. When the population is high there tends to be a greater proportion of males than when the population is low. This correlation, however, falls down in comparing the variations in the two curves for the second half of the period. The correlation is no better when the percentage of males among the one-year-olds is compared either with the population of the one-year-olds or the total population. It is probable that the factors causing these variations in the population affect both sexes in nearly a similar manner.

Environmental and other factors that may affect variations in abundance of the house wren have been analyzed for the years 1921 to 1934, inclusive, in two earlier papers (Kendeigh 1934, Kendeigh & Baldwin 1937). Of all the factors considered, temperature appeared to be most influential both in causing variations in yearly amount of reproduction and in yearly mortality. In Figure 2 the mean temperature on the wintering range during December, January, and February is plotted. A curve showing the mean temperature during the breeding season was drawn but is not here included as it showed no correlation with the population curve. A separate curve for temperatures during May gave somewhat more promise but did not correlate as well as the temperature curve for the winter. Average monthly precipitation and percentage of possible sunshine appeared unimportant during the breeding season. During the winter, precipitation was especially heavy during the years 1915, 1919, 1926, and 1936, which correlate with low points in the population curve, but it was not exceptional in 1940. Probably its influence is secondary or supplementary.

Winter temperatures preceding the breeding season were generally low from 1915 to 1921. This may explain the suggestion made earlier (pp. ???-???) that the colonization of this area by birds during these early years was not as rapid as would be expected for normally favorable conditions. Unfavorable weather conditions for birds in 1917 and 1918 have been noted by Cooke (1923). The peak in the population curve for 1922 and 1923 agrees with a rise in temperature during the winter which presumably would permit a greater survival of birds.

Drops in the population curve in 1924, 1926, 1931, 1936, and 1940 coincide with extreme drops in the temperature curve during these same years. Likewise years of greater abundance follow winters with milder temperatures although the degree of abundance seems not to correspond with the height of the temperature curve so long as temperatures are above a certain threshold. As shown in the figure this threshold may come at about 50° F. (13° C.). When winter temperatures average below this point, mortality becomes considerably higher, so that the breeding population the following summer is reduced. Actually, the greatest amount of this mortality may come during short periods of a few hours or days when temperatures are especially severe. The curve showing variations in number of one-year-old birds agrees with the temperature curve better than does the abundance curve for two-year-old birds.

Local shifts in the population of the house wren. In addition to factors, as climate, that may affect the abundance of a species, there may be local shifts of birds between neighboring areas as well as exchanges of individuals between the breeding and non-breeding populations. This can normally be ascertained only when there is identification of the individuals composing the population, as through banding. If a nest-site or territory is occupied throughout the breeding season, this may or may not be by the same adult individuals. If the territory is occupied by different individuals during the second breeding period than during the first, this should be considered in computing the total population that uses the area. This is especially true if birds present only part of the season do not nest elsewhere the same year.

Tables 12 and 13 are given to show the extent of shifts in the individual components of a population of the house wren that has two breeding periods a year (May-June and July-August). In this species, the male remates for the second brood, and the remating may be with a different female than he had for the first brood or it may be with the same one. During the 19 years with records, there was a change in identity of about 24 percent of the males and 28 percent of the females (average 26 percent all adults) between the first and second breeding periods, the number that disappeared from the 15-acre area was replaced by nearly the same number of new birds that came into the area. From trapping and banding operations in the surrounding region it is known that about 12 percent of those birds that appeared or disappeared between broods nested elsewhere the same year. This would be equivalent to only 3 percent of the total population. Thus the total number of birds that should be counted as nesting on the area at some time during the season was higher by 23 percent than would be indicated if the size of the population were measured simply by counting occupied nests, established territories, or number of adults present at any one time. The problem is of course simpler for those species that have only one brood during the year.

The non-breeding population of the house wren. Analysis of Table 12 permits computation of the percentage of singing males that do not secure mates for nesting. During any one breeding period this percentage is high, but taking the season as a whole, there is record of only 6 birds that went through both breeding periods without nesting out of 134 that were present on the area throughout the season.

TABLE 12. Summary of mating activity and changes in population of male house wrens between breeding periods each year on a 15-acre country estate.

Year	Present throughout season				Disappeared at end of first period		New birds second period		Died during first period	Polygyny		Total number
	Mated	Unmated										
	Both periods	First period	Second period	Both periods	Mated	Un-mated	Mated	Un-mated		First period	Second period	
1921.....	7	0	1	0	1	0	1	1	0	1	1	11
1922.....	3	0	2	1	3	2	4	0	1	0	1	16
1923.....	4	0	0	1	3	0	2	2	0	1	0	12
1924.....	4	2	1	1	1	0	0	1	0	0	0	10
1925.....	5	1	0	1	0	0	0	1	1	2	0	9
1926.....	2	0	0	0	0	0	1	1	0	0	1	4
1927.....	4	1	0	0	1	2	2	1	0	0	1	11
1928.....	4	4	1	1	1	0	0	0	0	0	1	11
1929.....	8	1	1	0	1	0	0	0	0	0	0	11
1930.....	3	1	5	0	1	0	1	1	0	2	0	12
1931.....	2	0	4	0	2	0	2	0	0	0	1	10
1932.....	5	1	1	0	2	0	1	0	0	0	0	10
1933.....	4	0	5	0	4	0	0	0	0	1	1	13
1934.....	3	3	2	0	2	1	2	0	0	1	0	13
1935.....	4	0	3	0	1	0	2	1	0	1	0	11
1936.....	5	1	1	1	1	0	1	0	0	0	1	10
1937.....	6	0	1	0	2	1	4	1	1	0	1	16
1938.....	4	1	1	0	4	0	5	0	0	0	0	15
1939.....	4	0	2	0	3	0	4	0	0	0	0	13
Total..	81	16	31	6	33	6	32	10	3	9	9	218

However there were 16 other males that left the area at the end of the first breeding period or appeared for the first time during the second period which did not secure mates while on the 15-acre area. Probably 12 percent or 2 birds out of these 16 secured mates elsewhere during the season. If the remaining 14 birds are added to the 6 that were unmated within the area, this represents about 9 percent that did not actually nest out of the 218 singing males that occurred on the area. Doubtlessly this figure will vary for different species, but it shows the potential degree of error when the population of breeding pairs is determined from counting only singing males.

In addition to unmated singing males, Tables 12 and 13 show that a fairly large number of both sexes mated and nested for only one of the two breeding periods and were, for the most part, non-breeding during the other period. This has been considered in the preceding section and by Kendeigh (1941a). Furthermore, there were some birds, comprising about 2 percent of the entire population, that did not appear at all during the season, although present in former years and nesting again in the area in later years. The presence of these non-breeding birds is often difficult to note, although an occasional individual may be seen lurking in the underbrush. The point is that when one measures the breeding population during only part of the season he does not measure the total population that may be present. The percentage of non-breeders at any one time in the total population doubtlessly varies in different species and may often be a substantial amount. This should be kept in mind in evaluating the population density of birds during the breeding season, as often only nesting pairs and singing males can be counted.

TABLE 13. Summary of mating activities and changes in population of female house wrens between breeding periods each year on a 15-acre country estate.

Year	Present and mated			Died during first period	Brood failures		Total number
	Both periods	First period only	Second period only		First period	Second period	
1921	7	1	1	0	1	1	9
1922	8	0	2	0	2	0	10
1923	5	3	4	1	3	0	13
1924	5	2	2	0	5	0	9
1925	5	2	1	0	3	1	8
1926	1	0	4	1	1	1	6
1927	5	0	3	1	2	2	9
1928	6	0	3	2	4	3	11
1929	8	1	2	0	4	1	11
1930	5	6	2	0	8	4	13
1931	3	4	2	0	3	2	9
1932	4	3	1	2	4	4	10
1933	4	8	1	0	10	2	13
1934	6	1	1	0	1	2	8
1935	6	2	1	0	5	3	9
1936	6	1	2	0	1	2	9
1937	7	3	3	0	2	3	13
1938	6	3	2	0	1	3	11
1939	6	2	2	0	3	0	10
Total	103	42	39	7	63	34	191

STRIP CENSUS OF TOTAL POPULATIONS

Literature. The strip over which a census is taken may be of a variable width or of a constant width. The type of results and the corrections needed in the use of strips of variable width depend on the conspicuousness of the different species and have already been discussed (pp. 73-76). In the use of strips of constant width, only birds are counted that fall within the boundaries of this strip and constant attention must be paid as to just where these boundaries fall. Usually this depends on the judgment, experience, and care of the observer.

Forbes and Gross (1907-1923) appear to have been the first to make strip censuses. Two men worked the strip together, one to call out the species and numbers, the other to do all the recording. These men maintained a distance apart of 90 feet in open country, but counted all birds flushed in a strip 150 feet wide, including those flying across the strip within 300 feet in front. Dense or tall forests were generally avoided and in orchards, open woods, and dense shrubs, the width of the strip was reduced to 60 feet. Pedometers mechanically recorded the distance covered. As a result of using this method an average of one bird per acre was recorded in midsummer in Illinois, giving a total for the state of 30,750,000 native birds and 5,536,000 English sparrows.

Cleland (1918) first used a strip a quarter-mile wide and attempted to count all birds, making arbitrary corrections for the less conspicuous smaller species. Later (1922), however, he considered strips of different width in computing the area censused for different species. He found on retracing the same route that he obtained similar counts as on the first time over.

Sundström (1927), Palmgren (1941), and other workers in Finland, Klocker (1936), Granit (1938), Kalela (1938), Soveri (1940) often used strip censuses, with one or occasionally two persons in a strip 130 feet (40 meters) wide. They combined this method with plot censuses. Palmgren states that the strip censuses were more useful during the winter or in situations where the birds were not too numerous.

The question as to the proper width of the strip that should be taken to record most effectively all kinds of birds is an important one. Breckenridge (1935) attempted to work this out in a scientific manner by traversing repeatedly over a square mile of mixed but mostly open wet habitats and recording the approximate distance at right angles to the line of travel at which each bird flushed. As a result of this study he used a strip 196 feet wide for computing the minimum density of birds on his area.

Saunders (1936) gives a figure for the total population of all species on 16,967 acres of varied forest

and second growth communities in Allegany State Park, New York. The population in each type of community was obtained from strip counts. He explains that his strip, 175 double paces long by 50 double paces on each side, equalled 10 acres. This is possible if his double pace was 5 feet long and the width of his strip 500 feet. In the experience of most other census-takers reported in the literature, this is too wide a strip for accurate results in forested areas.

In England, Lack & Venables (1937) made strip censuses of varying width in heath and dune both in winter and in summer for comparison of abundance. Winterbottom (1938) used a strip only 60 feet wide in his bird census in Rhodesian woodlands. In Ohio, Dambach and Good (1940) worked strips together with one man recording. In open fields, the width of the strips varied up to 150 feet depending on terrain, density of vegetation, and territorial aggressiveness of the birds. In woodlots the observers were 75 feet apart. Stops were made at 100 or 150 foot intervals to record singing males.

Reelfoot Lake, Tennessee. During late March or April each spring for the last several years a field trip has been conducted from the University of Illinois to the region of Reelfoot Lake in western Tennessee. The principle objective has been the study of the succession of biotic communities from open water to the climax. One phase of this study concerns the analysis of the bird population in each community both as to species composition and as to size. It is not our present purpose to discuss the species composition of each community but rather to give estimates as to the size of the total bird population.

Because of the nature of the trip, the fact that only one visit could be made to each community each year, and because the available time spent in each was limited, the strip census method was employed to determine the composition and size of the bird populations. In censusing open water the total size of the area was estimated visually. A pedometer to measure distance was regularly used but was not very accurate because of the observer's frequent change of pace and stops.

For forest communities the census was considered to cover a strip 150 feet wide. This width is too wide for accurate counting of some species and is not wide enough for others, but represents a reasonable average for all species. No attempt was therefore made to compute abundance of each species separately but only the total individuals of both sexes of all species. No attempt was likewise made to count only the individuals that occurred within the limits of this strip. The work was done with a small class of students desirous of seeing and recognizing as many birds as possible. In the case of the cypress swamp that was censused, the route lay along or just within the forest-edge with plowed fields on the outside. The strip censused here was considered to be only 100 feet in width. Other modifications or corrections were made as conditions demanded. Obviously the population densities obtained were approximate only, but they demonstrate changes from community to community. Table 14 is a summary of these censuses for the five years, 1937 to 1941 inclusive. The communities are named after their principle plant dominants, except for the open water.

TABLE 14. Size of bird populations in various communities at Reelfoot Lake, 1937-1941 inclusive.

Name of Community	Number of species	Population per 100 acres (40 hectares)		
		Average	Minimum	Maximum
Open water, Mississippi River	4	6	3	10
Open water, Reelfoot Lake	7	350	40	930
Open water, a slough	6	280	140	430
Willow-cottonwood-sycamore	21	410	220	620
Cypress Swamp	29	640	290	[illegible]
Hackberry-gum	32	390	[illegible]	680
Gum-oak-hickory	24	450	270	[illegible]
Beech	19	280	80	450

During some years the woods were full of transients on their way northward. Protected lakes and sloughs which had more abundant and obtainable food supply had more water birds than did the Mississippi river. At times large numbers of ducks, double-crested cormorants, American egrets, and great blue herons occurred in such places. The largest bird populations were found in the four forest stages from willow-cottonwood-sycamore to and including the gum-oak-hickory. Probably the differences between them in numbers of birds are not significant. The extra large number of birds in the cypress swamp may be due to their concentration along the forest-edge, which was the part censused, and so is not directly comparable with the other forest communities where the forest interior was the main portion studied. The low population in the climax beech community, that occurred on the upland bluffs and hills farthest from the lake, is significant as this difference was evident in every year of observation. Changes in the minimum and maximum populations observed during this period support the statements based on the average population. There were also changes from year to year in the size of the population in each community, but these will not be discussed.

CENSUS OF TOTAL POPULATIONS IN SAMPLE PLOTS

Size of sample plot. The size of the area taken as a sample of a community has varied with each worker and with circumstances. Jones (1898) obtained a winter census over 1.75 square miles in a village, Burns (1901) covered one square mile of varied country habitats during the breeding season. Saunders (1914) made a definite contribution by

making separate censuses in ecological communities of different character. Waters (1916) gives a census for a 40-acre farm, and the censuses obtained by the Cookes (1915, 1916, 1923, 1927) cover portions or entire farms of varied habitats. They recommend an area of 40 to 80 acres for censusing farmland, 10 to 20 acres for woodland, and 40 acres for portions of continuous forest. Nice (1927) censused a narrow strip of woods along a stream about one-half mile long and involving 40 acres. Tuovinsen (1936) covered 64 acres of spruce, pine, and birch woods. In mixed deciduous and evergreen forests Schiermann (1930) found 60 acres too large and so used quadrats, which he marked out with string, of only 15 acres, but he placed considerable emphasis upon the actual locating of nests as the basis for his census. Zimmerman (1932) obtained counts of birds over 10 years in a 54-acre marsh. Shaver (1933) made a detailed study of influence of weather factors on numbers of birds in a section of stream valley although he does not state the size of the area. Lack (1935) with the help of cooperators censused 1,700 acres of heath and grass. Hicks (1935) covered 80 acres of stream valley woods, locating nests and territories. Willams (1936) found an area of 65 acres of deciduous forest about the maximum size he could census accurately in a day. Van Deventer (1936) gives the winter population per square mile on the basis of 1,700 acres of abandoned farmland, forest, and swamp, although he surveyed only about 40 acres on each trip. Saunders (1938) had the help of students and reports censuses in four types of forests totaling 225 acres. Chapman (1939) covered 125 acres of farmland in England for both winter and summer bird populations, but he had the help of a line of several observers in the winter as they systematically covered the entire area. Turbott (1940) censused 75 acres during 10 days of the breeding season by walking back and forth and repeatedly localizing individuals on their territories. Kendeigh (1941) reports the breeding population on 50 acres of prairie. A larger area could have been covered as effectively if it had been available. Breeding bird censuses of the Audubon Magazine cover areas from less than 3 acres to over 250 acres in size. There have been censuses of all birds, terrestrial as well as marine, on small islands of various sizes (Murphy 1925, Wynne-Edwards & Harrison 1932, Harrison & Lack 1934, Southern 1938, Bergman 1939, Nicholson & Fisher 1940, Lack 1942, Vogt 1942).

The very high densities of nesting population reported by Grosvenor (1916) and Whitaker (1916) were due to their taking only one acre of optimum habitat around the house on country estates. Doubtless many if not all the birds that they included in their censuses regularly covered a much larger area. The same criticism applies to Pitelka's (1942) report of the birds nesting on 7.5 acres which he calculates at 2,300 birds per 100 acres. Sample plots must be large enough to include all the activities of all the species involved except possibly the larger predators.

The best size of the sample area to use for a detailed and careful census varies with the method to be employed, type of community or habitat, number of observers, abundance of the birds, and available area of uniform habitat. From the experience of many observers it appears that about 50 acres of forest and perhaps 75 acres of open fields or prairie is about the best size on which one person can efficiently count the breeding birds in a day's time. For wintering birds larger areas may be used.

As yet there has been little attempt at censusing during the migration periods. This would be considerably easier for song birds in the spring than in the autumn. Censuses during migration periods give merely the number of birds present at any one time. It would be very interesting and worthwhile, however, to estimate the total number of birds that pass through an area in migration. This would involve determination of how long individuals of various species stop over on their journey. Nichols (1921) made such estimates for migrating shorebirds, and Hawkins & Bellrose (1939) have begun such determinations for migrating waterfowl that use the Illinois River in the autumn.

Nest counts. Mention has already been made that Schiermann (1930, 1934) based his censuses of forest birds in large part on the actual location of nests in small sample plots of 15 acres each. Hicks (1935) found the nests of 76 percent of the pairs that he records for an 80-acre stream valley. Beecher (1942) made an intensive study of 482 acres of marsh and upland based largely on location of nests. In his year of most intensive effort, 1937, over 85 percent of the nests of the breeding birds were actually found and plotted on a map. The approximate location of the remaining nests was obtained by repeated mapping of singing males. He counted only first brood nests in computing population densities.

In open country, as grassland, the use of a long rope is very helpful in finding nests. The rope should be as long as can be comfortably handled by one person at each end (100-150 ft.) and pulled transversely back and forth across the field. The rope should be heavy enough to drag over the top of the grass in a long shallow loop between the two persons at the ends. It is helpful to have additional persons walk behind the rope, spaced at equal distances, in order that all birds will be flushed from their nests and be quickly spotted. When a bird is flushed, the rope should be immediately dropped and careful search be made around the place where the bird rose. The use of ropes in this manner is widely known (Lack 1935). In a study of the birds in a prairie community in northwest Iowa, Kendeigh (1941) found it very efficient in locating nests of incubating pheasants, bobolinks, and western meadowlarks but had no success with it for grasshopper sparrows, although the birds were repeatedly flushed.

At the Baldwin Bird Research Laboratory, systematic search was made each year for nests of all species on the 15 acres immediately around the laboratory. This is a country estate, a man-made forest-

edge type of habitat, containing a maple grove with dense undergrowth, shrubs of many cultivated varieties, shade trees of many sorts, lawns, gardens, orchards, and buildings. A surplus of boxes were always available of sizes suitable for house wren, bluebird, English sparrow, starling, and other species. Never were all the boxes utilized at one time. With ample and varied nest-sites, cover, food, and some protection from predatory enemies, the nesting population was unusually high, averaging about 96 pairs during the years 1934 to 1939 inclusive. At least twice each year, sometimes three times, a systematic search was made by two to five observers through all the shrubbery and into all the lower trees on the area. This search was always a thorough one and it is doubtful if many nests were missed except possibly in the higher trees of the maple grove.

Offhand it might seem that finding nests is a positive and accurate method of censusing bird populations. This is not always true. Many species in this area had two or more broods per year for which they either built separate nests or re-used the old one. Other species had only one brood. Some nests were built and abandoned without being used. Others were used but then abandoned when the eggs or young were disturbed, and then another one was built for a second attempt. An effort was made to allow for all these various factors in using number of nests for computing the number of nesting pairs, but there was always some human equation involved in the final figures. Then for some species, like the ruby-throated hummingbird or those species nesting in high trees, the nest count was not accurate. This method is not practicable in forest habitats, as attempts to use it in such areas quickly demonstrated. Too few nests of known breeding birds can actually be located, and those that are found are usually by accident or after an undue expenditure of time.

Table 15 gives the number of nests found each year for the more common species. A study of this table shows that most species started with relatively low numbers of nests in 1925, and low numbers again occurred in 1930-31 and in 1939. Nests were most numerous around 1927 and again in 1934 or 1935. The starling first appeared as a breeding bird in 1929. Nests of the English sparrow were destroyed as soon as located.

Although there seems to be some agreement between several species in time of occurrence of large and small number of nests, this agreement is not close and is of uncertain significance. No correlations were found with variations in temperature, rainfall, or sunshine during the breeding season. Probably in analyzing causes for fluctuations in size of populations, each species should be considered independently and for all seasons of the year as was done for the house wren (pp. ???-???). No two species are identical in their toleration of extremes in environmental conditions, in the time that they are exposed to such conditions, in their migratory movements, in their wintering range, in their resistance to disease, etc.

Before such analysis can be seriously undertaken, one should ascertain how broadly the sample area represents the response of the species as a whole. This was done for the house wren (Kendeigh & Baldwin 1937) for an area of about one and one-half square miles in the vicinity of these 15 acres of concentrated study, and for the year 1926 and 1940 the evidence was good that similar low populations occurred widely throughout the eastern half of the breeding range of the species. For the other species listed in Table 15, a similar check was attempted by comparing yearly variations in number of nests in this region during the years 1925 to 1933, inclusive, with variations in number of nesting birds given by Hicks (1935) for an area only about one hundred miles to the south. These figures are not repeated here, as the variations in population of no species in the two areas showed any consistent correlation. If we assume that the census in each area was done with equal care and accuracy, then the only conclusion seems to be that most yearly fluctuations were due to variations in local conditions. No attempt is made to analyze at this time what particular local conditions were effective. Very probably there is not sufficient information available to do so for most species.

Counting singing males and mapping territories. Cooke (1927), who followed the same methods recommended in early years by the U. S. Biological Sur-

TABLE 15. Number of nests per year on a 15-acre country estate.

Species	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939
Mourning Dove	8	8	8	4	5	2	0	1	4	7	8	6	5	0	1
Phoebe	3	1	1	2	1	2	2	2	2	2	5	3	2	3	2
House Wren	8	6	9	11	11	13	9	10	13	8	9	9	13	11	10
Catbird	8	16	24	14	24	16	13	11	14	16	10	9	8	8	9
Robin	31	36	48	36	35	32	35	51	53	56	56	32	23	24	30
Bluebird	3	2	3	4	6	3	2	2	5	2	1	1	1	4	3
Starling	0	0	0	0	1	2	6	1	3	8	10	11	8	4	2
English Sparrow	5?	18	15	3?	8	8	3	4	11	16	31	30	20	19	18
Chipping Sparrow	7	17	19	12	10	12	9	7	9	14	12	14	16	12	7
Song Sparrow	7	3	18	11	5	4	18	15	18	28	10	8	6	6	7
Miscellaneous Species	14	10	21	13	6	15	18	13	12	24	25	12	21	14	13
Total	94	117	166	110	112	109	115	117	144	181	177	135	123	105	102

vey, describes "a convenient way of taking a bird census is to count the singing males very early in the morning. At this time every male bird is usually in full song near the nest site; and after migration is over, each one may safely be considered to represent a breeding pair." This method has also been adopted by the Finnish ornithologists, Sundström, Palmgren, and others.

There have been serious criticisms of counting singing males as representing nesting pairs in that a sizeable percentage, 9 percent in the house wren, may be unmated; that males after they acquire a mate and start nesting often reduce their singing or stop altogether; and the amount and intensity of singing varies between species. In spite of these objections the recording of singing males is essential in any method of censusing, although such data should be supplemented with other information. Often it is impossible or very difficult to make certain whether a male bird, singing but unmated at one time, actually remains unmated throughout the breeding season, so it is usually justifiable to let all singing males represent at least potential breeding pairs. This may be a reasonably reliable index of possible carrying capacity even if a few males never do mate (Kalela 1938).

In making a census of a plot it is necessary, of course, to visit all portions, and preferably this should be done in the morning as there is generally a decrease in activity and conspicuousness of birds during the middle of the day. In explaining his method, Palmgren in 1929 stated he traversed his forested areas in parallel lines 50 meters (162 ft.) apart. The writer has found this the maximum distance that can ordinarily be used efficiently. Considerable time is saved when a line of observers can simultaneously move through an area, provided care is taken that the same bird is not counted by more than one observer.

The use of maps in making bird censuses is very desirable. Jones used such a map to record location of birds in his winter census of 1898 and they have been employed by several recent observers (Lack & Venables 1937, Saunders 1938, Chapman 1939, Beecher 1942). Williams (1936) developed through the use of maps a good method of censusing by the approximate delimitation of territories. He had a series of mimeographed maps of his area with trails and other guide signs incorporated. On each weekly visit he took a new map and marked each bird seen. At the end of the season he made a composite map for each individual species, showing the location of all individuals seen on all trips. These locations fell in groups indicating territories, so he could readily count the number of pairs with some accuracy. For some species he was able to verify his census by finding nests the following winter on the territories he had marked out. This method does not distinguish unmated birds nor all changes in adults or territories when second broods are raised. Occasional records of isolated individuals may be disregarded, as they may be intruders from elsewhere or birds temporarily away from their territories. It has the advantages of being relatively quickly conducted, although it requires repeated visits to the area. Also it allows the territories to be identified by the presence of either males or females and their verification by location of nests. Unless a large number of trips are made the true size and boundaries of the territories may not be determined with great accuracy, but this is not the main purpose of the method. This method has been followed by Kendeigh (1941) and in the present paper (Figures 3, 4).

Frequency of surveys. The frequency with which a plot should be surveyed for a breeding bird census must be considered. Cooke (1927) recommends that the area should be surveyed at least twice during the height of the nesting season, more often if possible. Recommendation that the census not be taken until after June 1 is at fault, as Nauman (1926) indicates, because some birds are through nesting by that time. In his census of farmland throughout the year, Wild (1935) surveyed the area on 56 visits. Palmgren (1930) carefully investigated the number of trips required for a complete census. He took periodic trips to the same area, and to compute the total population of birds present he totaled the maximum number of each species recorded on any single trip regardless of the trip on which it was obtained. Thus he found that one survey through an area ordinarily listed only about 62 percent of the total population eventually found to be present, two times over the area increased the count to 80 percent, three times to 91 percent, and four times to 96 percent. He has such confidence in these figures for his region that he has reported populations based on a single survey with the figures corrected accordingly (1931).

At the Edmund Niles Huyck Preserve, Rensselaerville, New York, the writer had an opportunity during the summer of 1942 to check the correction factors used by Palmgren. A census of the breeding population in a 21-acre hemlock-beech forest was made by repeated and systematic cruising over the entire area during the height of the breeding season. A half day was spent for each count as all birds were spotted on a map of the area, territories were mapped, and behavior observed. This is explained to emphasize that considerable care was taken to get accurate totals, and methods were used in addition to simple cruising or strip counting to which Palmgren confined himself. Counting the largest number of individuals of each species recorded on any trip, it will be noted (Table 16) that with each successive trip a larger number of birds was recorded, although the percentage of increase gradually declined. Sufficient observations were taken on other days than those indicated so that the total population as given was verified by repeatedly finding the birds on their mapped territories and there was little chance of duplication or inclusion of transient individuals. Compared with Palmgren's figures, one more survey was required to obtain approximately the same percentage of the ultimate total population, that is, five trips instead of four were required to get 96 percent

TABLE 16. Results of repeated bird counts (number of potential pairs) on 21 acres of hemlock-beech forest in New York State.

Species	June 6	June 10	June 13	June 18	June 23	June 26	Total
Oven-bird	6	6	8	10	10	10	10
Black-throated Green Warbler	5	6	6	7	5	5	7
Magnolia Warbler	2	5	5	5	5	5	5
Blackburnian Warbler	3	4	4	4	4	4	4
Canada Warbler	1	2	2	3	3	3	3
Hermit Thrush	2	1	3	0	0	0	3
Black-throated Blue Warbler	1	1	1	2	2	2	2
Black and White Warbler	0	0	0	1	2	0	2
Black-capped Chickadee	0	0	1	1	1	2	2
Hairy Woodpecker	1	0	0	0	0	0	1
Pileated Woodpecker	1	0	1	0	0	0	1
Robin	1	1	1	0	1	0	1
Blue Jay	1	1	1	0	1	0	1
Scarlet Tanager	0	1	1	1	1	0	1
White-breasted Nuthatch	0	0	0	1	1	0	1
Red-eyed Vireo	0	0	0	0	1	1	1
Veery	0	0	0	0	0	1	1
Crow	0	0	0	1	1	0	1
Ruffed Grouse	0	0	1	1	0	0	1
Great Horned Owl	0	0	0	0	0	1	1
Progressive total	24	31	37	45	47	49	49
Percentage of ultimate total	49	63	76	92	96	100	100

of the total population. A few species had completed their nesting at the time the first census was taken.

As the result of these studies, it would seem desirable in getting total numbers of all species during the breeding season in middle latitudes of North America to take one count in late April, at least one in middle or late May, two or three in June, and at least one toward the middle of July. It is recommended that five complete counts be considered a minimum and these be well spaced through the nesting season.

Trelease Woods. Bird censuses at all seasons have been conducted for a number of years in Trelease Woods at the University of Illinois near Urbana, Illinois, by Dr. V. E. Shelford, who initiated the work, the writer, Dr. H. H. Shoemaker, and graduate students, *viz.*, Dr. S. A. Hyde, Dr. A. C. Twomey, R. G. Lindeborg, Dr. Sarah Jones, J. Murray Speirs, H. C. Seibert, Verna Johnston, Dr. T. W. Roberts, and Dr. C. T. Black. Of these, Dr. Hyde, Dr. Black, Dr. Twomey, and Miss Johnston have manuscripts which will, when published, give further information on the bird populations for particular years. Data for the winter of 1924-25 comes from Blake (1926).

These yearly censuses have concentrated on getting the wintering and the breeding populations, although some effort has been given to getting populations during the migrating season as well. To facilitate this census over the 55 acres, the woods in 1939 were marked out into squares by permanent stakes set 50 meters (162 ft.) apart in each direction. The stakes rise 3 ft. above the ground, are painted yellow, a wide yellow ring is painted on the nearest tree at a somewhat greater height, and each stake is numbered. Mimeographed maps have been prepared showing the numbered stakes so that the location of any bird, nest, or other object may be quickly and accurately plotted (Figures 3, 4). The location of all birds were mapped as the observer followed along each line of stakes and totals for each species determined at the end of each day when the maps of the different observers who participated were combined into one. Mapping the location of each bird helped to prevent

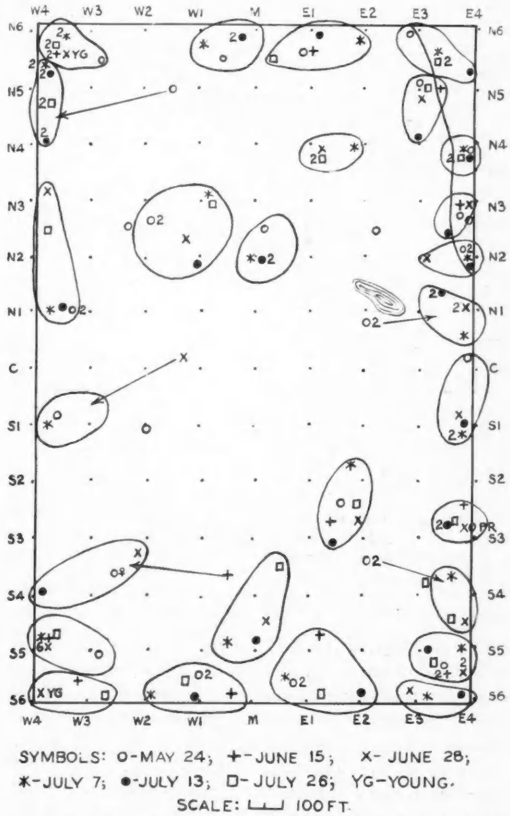

FIG. 3. Composite census map for the indigo bunting in 1942 showing how points where birds were observed on successive dates aggregate into distinct groups, indicating the identity of particular adults on their territories. This is primarily a forest-edge species although five pairs occurred in the forest-interior.

duplication of counts during the winter and permitted outlines of territories during the summer. To get the breeding bird census the method worked out by Williams, described above, was used. Two trained observers required 3-4 hours to complete a survey

during the breeding season and about two hours during the winter. Morning proved by far the best time for this work.

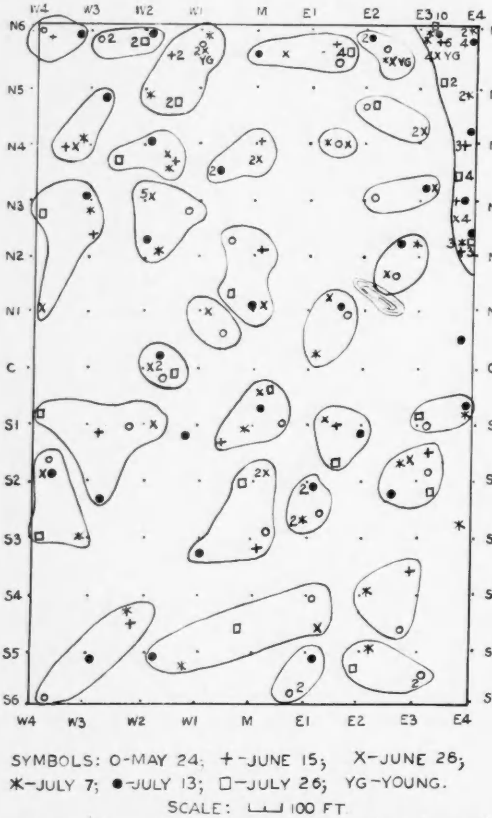

FIG. 4. Composite census map for the house wren in 1942 showing how points where birds were observed on successive dates aggregate into distinct groups, indicating the identity of particular adults on their territories. Note the uniform dispersal of the species through the forest-interior with no relation to the forest-edge.

Table 17 gives the data on the breeding population of these 55 acres. The table includes forest-edge as well as forest-interior birds. The forest-edge of low trees and shrubs is narrow except in the northeast corner. The observer usually went entirely around the area at the beginning of his survey, looking into the forest and counting the birds as seen on the outside of this forest-edge, then he transversed back and forth lengthwise through the interior of the forest. The censuses were not as carefully nor as accurately done some years as others and this is indicated in the table. Although the censuses go back to 1927, several years were omitted.

The following additional species were represented by one or two pairs, but too infrequently to include in the table: sparrow hawk, 1937; blue jay, 1927, 1928, 1943; white-breasted nuthatch, 1934, 1936; Carolina wren, 1934, 1943; robin, 1927, 1936; blue-gray gnatcatcher, 1928; oven-bird, 1937, 1943; Kentucky warbler, 1928; redstart, 1928; towhee, 1934, 1935.

In general, there has been an increase in the abundance of breeding birds in this area during the last 15 years. The area was purchased by the University of Illinois in 1917-1918 and has been allowed to return to an undisturbed condition. Previous to that time there had been some rather heavy grazing by domestic stock in the woods and some trees had been removed, but it had never been completely cut over. It is possible that the better development of the shrub stratum, young trees, and forest-edge, may be responsible for this increase in birds as well as the leaving of dead trees and limbs, with their offering of nest-sites, for hole-nesting species. The red-eyed vireo and crested flycatcher have been perceptibly more abundant during the last three years as compared with the first six, but the increase in the size of the total population is due in large part to the invasion of starlings and house wrens. Starlings first appeared in the vicinity in the winter of 1921-22 (Smith 1922) but did not invade this woods until several years later. Only a single pair of house wrens was recorded in the woods during 1927. In 1934 and 1935 they were present only during the second breeding period from late June through July. Beginning in 1937, however, this species has increased in numbers to such an extent that it challenges the indigo bunting as the most abundant species in the community. There is some evidence, on the other hand, that the red-headed woodpecker, cardinal, and perhaps the wood thrush have decreased in numbers in recent years.

Table 18 furnishes data on number of individuals wintering in Trelease Woods. No species is included that was not present well through January, the coldest month of the year. This excludes some late migrants that lingered into December and early migrants that arrived in February. The table also excludes species seen on only an occasional trip during any winter. Some species occurred throughout the winter for only one, two, or three years, and these are here lumped together as "irregular species." These species include rough-legged hawk (1927-28), red-breasted nuthatch (1941-42), Carolina wren (1928-29, 1942-43), purple finch (1926-27, 1927-28), common redpoll (1924-25, 1933-34), goldfinch (1927-28, 1929-30), and fox sparrow (1927-28, 1928-29, 1929-30).

Since the wintering population is less stable than the breeding population, on account of migratory and local movements, the arrival at a figure for the number of individuals of the species presents some difficulties. Data are included in the table only for the months of December, January, and February. When the population of a species varied considerably and irregularly during this three-month period, a simple average of numbers seen on all trips was used. With most species, however, the numbers recorded on successive trips varied around a medium as follows: 5, 6, 4, 6, 6, 6, 5, 7, 4, 5, 5, 8, 6, 6, 5, 14.

TABLE 17. Number of pairs of breeding birds, Trelease Woods, Urbana, Illinois (55 acres), with indication whether they belonged primarily to the forest-edge (E) or forest-interior (I).

Forest niche	Year / Rating of data	1927 Fair	1928 Fair	1934 Good	1935 Good	1936 Fair	1937 Fair	1939 Poor	1940 Fair	1941 Good	1942 Good	1943 Good	Average
E	Cooper Hawk	1	1	0	1	0	0	0	0	1	1	1	0.6
E	Mourning Dove	1	1	0	2	2	0	0	0	0	0	0	0.6
I	Yellow-billed Cuckoo	1	3	1	2	2	1	0	0	3	4	5	2.0
I	Barred Owl	1	1	1	1	1	1	1	0	0	0	0	0.6
E	Ruby-throated Hummingbird	1	1	1	1	1	1	1	1	1	1	1	1.0
E	Flicker	1	0	1	1	2	1	1	0	0	1	1	0.8
I	Red-bellied Woodpecker	1	1	0	0	1	0	1	1	1	0	1	0.6
E	Red-headed Woodpecker	1	0	4	2	3	5	1	1	0	0	1	1.6
I	Hairy Woodpecker	1	2	1	1	1	0	1	1	1	1	1	1.0
I	Downy Woodpecker	2	3	5	4	2	4	1	4	5	5	6	3.7
I	Crested Flycatcher	4	4	5	4	5	5	–	11	7	8	7	6.0
I	Wood Pewee	3	7	3	4	7	6	6	8	10	5	8	6.1
E	Crow	2	4	2	5	4	2	1	6	2	4	9	3.7
I	Tufted Titmouse	2	5	5	4	6	4	3	3	2	2	3	3.5
I	House Wren	1	0	3	4	8	14	–	10	20	31	40	13.1
E	Catbird	2	0	1	1	1	0	0	0	0	0	0	0.5
E	Brown Thrasher	0	0	1	1	1	0	0	0	0	0	0	0.3
I	Wood Thrush	4	4	3	3	2	2	–	1	1	2	2	2.2
E	Starling	–	–	8	10	25	16	–	5	9	12	15	12.5
I	Red-eyed Vireo	9	7	8	4	4	5	–	–	13	14	10	8.2
E	Yellow-throat	0	0	2	1	1	1	–	5	1	1	2	1.4
E	Cardinal	3	5	3	3	2	2	1	2	1	2	3	2.5
E	Indigo Bunting	17	9	22	21	20	20	–	15	25	27	27	20.3
E	Goldfinch	–	–	2	–	10	–	–	–	4	1	3	4.0
E	Field Sparrow	0	0	2	2	0	0	0	0	0	2	1	0.6
E	Song Sparrow	0	0	1	1	0	0	0	0	0	1	0	0.3
E	Irregular Species	2	5	4	1	3	2	0	0	0	0	3	1.8
	Total (excluding cowbird)	60	63	89	84	114	92	–	–	107	125	150	99.5

In this case it appeared that 6 birds indicated the resident population. On some trips individuals were overlooked. On other trips some individuals may have been counted twice, or there may have been a temporary influx from the outside.

In general, there appears to have been no marked change in the total size of the wintering population during the last 18 years. The downy woodpecker and red-bellied woodpecker have increased in abundance while the cardinal, as during the breeding season, has been present in smaller numbers in recent years. The permanent resident species are, in general, somewhat more abundant in the woods during the winter than during the summer. This is particularly the case with the flicker, blue jay, and white-breasted nuthatch.

Northern Ohio. During the winters of 1938-39 to 1941-42, inclusive, members of the Cleveland Bird Club made repeated surveys over sample areas from December to February. These areas were of known size and each represented a special community. At the end of the winter the total resident population was computed, excluding the wanderers and transients. Twelve reports for open country, that varied from marsh to grassland to a country estate, included 430 acres for a total of 643 birds. This is a density of 150 individuals per 100 acres. Eight reports in forest habitats covered 357 acres for a total of 292 birds. This gives a density of 82 individuals per 100 acres.

For wintering bird censuses in the Cleveland region, the population densities obtained from sample plots is probably too high. For open country habitats, the size of these sample plots varied from 15 to 103 acres. For some of the small areas the density ran extremely high; for instance, one 15-acre marsh contained 92 birds of which 80 were tree sparrows. Very likely this flock of tree sparrows wandered during the winter over a larger area than figured in the census. Likewise, since this plot was small there is no guarantee that it was representative for this habitat. Another 15-acre area selected at random could conceivably have had no birds. To test the importance of size of sample plot censused, seven reports for areas from 37 to 103 acres in size were averaged separately, and this density proved to be only 53 individuals per 100 acres.

Sample plots of forested areas in the Cleveland region varied in size from 26 to 75 acres and averaged 44 acres. The average size is a little low but not excessively so. In any case corrections need to be made for species that require larger areas than were censused and also for species confined to the forest-edge.

TABLE 18. Number of birds in wintering population, Trelease Woods, Urbana, Illinois (55 acres), with indication whether they belonged primarily to the forest-edge (E) or forest-interior (I).

Forest niche	Year	1924-25	1926-27	1927-28	1928-29	1929-30	1933-34	1934-35	1935-36	1937-38	1938-39	1939-40	1940-41	1941-42	1942-43	Average
	Number of censuses	18	?	10	?	?	16	19	14	4	7	6	5	5	5	....
E	Red-tailed Hawk	1	2	2	1	0	2	2	1	1	1	1	1	1	1	1.2
E	Bob-white	0	0	0	0	0	0	0	0	13	0	3	6	0	0	1.6
E	Mourning Dove	0	0	0	0	0	0	0	10	0	6	14	0	0	0	2.1
E	Barred Owl	0	2	2	2	2	0	0	0	0	1	0	0	0	0	0.6
E	Flicker	5	4	7	6	9	2	8	4	3	5	1	0	2	0	4.0
I	Red-bellied Woodpecker	1	1	2	1	1	0	0	0	3	3	1	2	2	3	1.4
I	Hairy Woodpecker	2	2	2	1	1	0	0	0	2	1	2	1	2	2	1.3
I	Downy Woodpecker	3	2	3	3	3	6	5	10	7	11	7	8	9	10	6.2
E	Blue Jay	5	2	0	1	0	2	2	2	2	1	3	2	10	6	2.7
E	Crow	5	3	12	0	4	2	20	0	8	6	10	18	5	6	7.1
I	Black-capped Chickadee	2	0	1	0	0	2	0	0	0	0	0	0	0	0	0.3
I	Tufted Titmouse	8	4	8	1	4	10	12	10	14	8	3	2	7	14	7.5
I	White-breasted Nuthatch	1	1	4	3	0	2	2	4	2	2	2	0	2	2	1.9
I	Brown Creeper	0	2	1	2	0	0	0	10	0	4	3	2	3	3	2.2
I	Golden-crowned Kinglet	1	0	2	0	0	0	0	0	0	1	0	0	0	0	0.3
E	Starling	0	0	0	0	0	0	0	20	2	2	1	0	0	0	1.8
E	Cardinal	5	16	12	4	4	10	10	6	2	2	1	1	3	1	5.5
E	Slate-colored Junco	15	25	20	3	1	10	10	85	0	0	5	0	9	0	13.1
E	Tree Sparrow	10	11	47	25	0	10	20	50	25	10	10	20	24	0	18.7
E	Song Sparrow	0	2	3	0	2	0	0	0	0	0	0	0	0	0	0.5
E	Irregular Species	2	7	13	2	5	10	0	0	0	0	0	0	1	1	2.9
	Total	66	86	141	55	36	68	91	212	84	64	67	63	80	49	82.9

Computation of population density. Problems concerned in computing the density of population can best be illustrated by consideration of the censuses made in Trelease Woods. On the basis of average total wintering population each year (83 individuals) on the 55 acres, the density would be 151 per 100 acres (Table 18). However, when one analyses the population by species, he soon realizes that this expression of density is not justified. The red-tailed hawk used the forest-edge as a roost and look-out and hunted over a large area of adjacent fields. The mourning dove was usually in the forest-edge and the bob-white always there, and both species more often fed and wandered into the fields and fence-rows than into the woods-interior. The barred owl was more nearly a true forest bird than the hawk yet the owl doubtlessly often hunted elsewhere. The flicker, blue-jay, crow, and starling were found throughout the woods but they were not confined to it and were often seen to fly long distances outside. The cardinal, junco, tree and song sparrows, and most of the irregular species frequented the forest-edge and were seldom found in the forest-interior. The junco and tree sparrow sometimes occurred in large flocks in the adjacent weedy fields. The other species listed in the table are the only forest species in the strict sense in that their activities of feeding and roosting were largely limited to it. Taking these forest interior species by themselves, a density of only 39 individuals per 100 acres is obtained. When lumbering opens up a forest or fragments it into small patches like this one, the edge effect becomes greatly exaggerated. Birds frequenting the forest-edge are really in another community and have developed quite different mores. They utilize their easy access to the forest for roosting, shelter, and some feeding and to open fields for the rest of their feeding and activities.

The same situation holds during the breeding season (Table 17). For an exact study during the nesting period, territories may be mapped and corrections made for individuals with territories that extend outside the boundaries of the forest proper. For instance (Figure 3), of the 27 pairs of indigo buntings listed for 1942, only 5 occurred in the forest-interior. The rest appeared dependent on the presence of the forest-edge. The house wren, although often considered a forest-edge species, occurred uniformly throughout the area and showed no such dependency (Figure 4). Making these corrections the density during the breeding season is reduced from 171 pairs per 100 acres to 91 pairs per 100 acres.

During the winter season there were 61 individuals present in the forest-edge and during the breeding season there were 48 pairs in this habitat. The length of the edge around this 55-acre forest is 6,570 feet or 1.25 mile. In order to arrive at some common denominator for comparing the abundance of forest-edge species, it may be necessary to use length rather than breadth. Probably no two species concur in the extent that they use either the forest or the open fields. At times a forest-edge is quite broad and in the form of an open forest or shrubby field. In such cases it is best to compute density in terms

of area, but for narrow edges around fragments of forest this must wait until the extent and significance of the forest-edge can be studied more intensively. Meanwhile it may be desirable for a general standard to base comparisons on the unit length of one kilometer (0.62 mile). Then the density of the bird population at Trelease Woods during the breeding season may be expressed as 91 pairs per 40 hectares (100 acres) of forest plus 24 pairs per kilometer (38 pairs per mile) of forest-edge, while in the winter it is 39 individuals per 40 hectares (100 acres) of forest plus 30 individuals per kilometer (49 individuals per mile) of forest-edge. If the number of pairs during the breeding season is doubled to indicate individuals, then the density of the summer population is found to be 4.7 times greater than in the winter in the forest-interior and 1.6 times greater on the forest-edge.

In computing the population density of all species of birds over large areas, such as counties, states, or even countries special care must be taken that the necessary census plots actually present adequate samples, in respect to percentage of the total area, number of censuses taken, and period of time covered. Davis (1942) presents some statistical considerations in this respect. Finnish ornthologists (Palmgren 1930, etc.) have been quite inclined to convert their figures obtained from samples into number of birds over large districts, although Forbes (1913) long ago did the same for the state of Illinois, Cleland (1918) on a smaller scale did it for New South Wales in Australia, and Saunders (1936) for Allegany State Park, New York. James Fisher (1939) facetiously even estimates from compiled censuses the total population of the world at 100 billion birds.

Either of two procedures may be followed. Sample plots may be established at uniform intervals along lines at uniform distances apart to form a grid pattern over the region as a whole. This would tend to eliminate the human element in selecting representative sample plots, as all types of communities would be sampled in proportion to their frequency of occurrence, provided a sufficient number of samples were taken.

The other procedure is to determine the average population density in selected communities of various types. Then the total population in the region can be computed if the area covered by each of the various types of communities is known. There are various difficulties in this procedure. Major community types vary in minor inconspicuous ways which may affect the density of the bird population but which often cannot be properly evaluated without first measuring the bird population. There are many varying types of communities as far as vegetation is concerned which may or may not coincide with differences in the population of birds. Finally the measurement of the area covered by each community is no small undertaking in itself.

The second procedure is usually the one used because there is more scientific interest and intrinsic value in knowing the population density in biotic communities of various types than in knowing the actual total population in large districts, which may be political units, although this latter knowledge is important in the formulation of management policies and conservation regulations. If the second procedure is used the proper designation and delimitation of the various types of communities becomes a matter of great importance.

Since there are often marked variations in abundance of birds from year to year, a census for a single season cannot assuredly represent the true density and specific composition of birds in any community. These variations in abundance from year to year may be cyclic, eruptic, progressive, or irregular and off-hand it would seem that at least 10 years record would be desirable to fix with some confidence the status of each species in a community. There are very few such censuses available (J. J. Hickey 1943).

Recognition and designation of the community. In recording the satus of birds in any region it is fully as important to designate properly the biotic communities in which they occur as to indicate their relative abundance or actual density. A community in the ecological sense is a unit organization of plants and animals with common characteristics throughout. Communities may be of any size, and different types of communities are given different ecological classification and nomenclature. The recognition, description, and naming of communities are not easy and require proper experience and knowledge of the literature (Shelford 1926, Weaver & Clements 1929, Clements & Shelford 1939). Cover mapping is, however, possible on a simpler basis if the requirements of a particular species is all that is concerned (Wight 1934).

Communities change as one replaces another until the climax is reached which persists indefinitely as long as the climate remains the same. Progressive community replacement is called succession; for example, pond—marsh—swamp shrub—swamp forest—climax forest. Successions are different as they occur in different habitats or in different climatic regions. Since the life-form of a plant varies more or less with the species, it is desirable to designate each community not just by the general life-form or type of the dominant vegetation but also by two or three of the most important plant species, *viz.*, balsam-black ash bog, cattail-sedge marsh, buttonbush-alder swamp shrub, oak-hard maple deciduous forest, pine-hemlock evergreen forest, etc.

Where two communities of different plant life-forms come into contact and intermingle there is a meeting of animal species characteristic of each community as well as additional species that require such a combination of two vegetation types before they occur at all. Thus there may be oak-hickory-pine forests, beech-hemlock forest, and the forest-edge may be designated as a forest-grassland community, or better, a forest-grassland ecotone to emphasize its transition or complex nature.

Animal relations must be considered for the recognition of the complete communities as biotic units. For instance, Beecher (1942) bases his study of nesting populations of birds principally on secondary plant communities (consocies) which are subdivisions of larger communities (associes). This is proper for analyzing factors controlling nest-site and nest-structure, but many species of birds that he lists for particular subdivisions regularly feed, roost, or carry on part of their activities in other subdivisions. For computing population densities (as distinct from nest densities) the entire area or series of secondary communities which the birds use must be considered as the biotic unit or community. Thus there are fewer biotic communities of this rank in a region than there are plant communities. Beecher recognized 17 secondary communities for purpose of studying nest distribution. For computing population densities of birds probably only four should have been recognized, *viz.*, lake and pond marsh, high prairie, oak-hickory forest, and forest-edge. Even with this simplification, certain species as the red-winged blackbird, extend their activities into two or more communities and their densities should be computed on the basis of still larger units.

When the unit study is the community, there should be as complete as possible description of the community concerned: area of forest-interior; length of forest-edge; density, size, life-form, and uniformity of distribution of the plant dominants; extent of undergrowth; amount of disturbance from original primitive condition; principal animal constituents; climatic factors, etc.

Separate lists and discussion should be given for each different community. This should be a major point of concern. The report on bird censuses conducted by the United States Biological Survey, 1916 to 1920 (Cooke 1923), is of considerably lower value because birds found in several kinds of communities are grouped together in the same list. The breeding bird censuses now being conducted by the Audubon Magazine are a considerable improvement although the forest-edge population is not always separated from that of the forest-interior.

This paper will not attempt to summarize the results of all population studies to date. Lack made a preliminary compilation of population data from the world's literature in 1937. Audubon Magazine usually makes a compilation each year of the data that they have accumulated for different major types of communities. The files of the Fish and Wildlife Service probably contain much unpublished information. The bibliography of this paper, while primarily concerned with methods of measuring bird populations, will nevertheless provide a good lead to the literature on data accumulated from such measurements. In order to analyze how compilations from various sources may be conducted and some of the problems involved, data on the constitution and density of the bird population in the deciduous forest of eastern North America will be brought together.

Birds of the climax deciduous forest. The deciduous forest biome varies regionally so that its climax may be communities dominated by oak-hickory, oak-chestnut, beech-hard maple, or mixed mesophytic, depending on the climate (Pitelka 1941, Braun 1942). In the oak-chestnut community, chestnut has recently almost disappeared on account of a blight, so that the present forests are dominated by various species of oaks, tulip trees, etc. This present compilation is intended to show the kinds and densities of breeding birds in the mature climax forest as little disturbed as possible from original primitive conditions. No entirely virgin areas remain, and the only usable data, according to our standards, that have been found in the literature come from the breeding-bird censuses of the Audubon Magazine (Hickey 1942).

All censuses dealing with deciduous forests have been analyzed and a number immediately eliminated for various reasons: they clearly dealt with successional communities rather than the climax, the forest was immature in its development after having previously been cut-over, the forest was being grazed, the forest was an open woodlot, the data on nesting was incomplete.

The censuses that survived this elimination process were next analyzed as to the degree that they included true forest birds or were infiltrated with forest-edge species. Species known to confine all their activities to the forest, *viz.*, territory, nesting, feeding, roosting, etc., are listed in Table 20 and these were well represented in most reports. Forest-edge species that may nest in the woods but also require grassy or shrubby fields, open forests, or other external habitats for their complete activity varied greatly from one report to another and included the following species: wood duck, Cooper hawk, red-shouldered hawk, ring-necked pheasant, mourning dove, black-billed cuckoo, ruby-throated hummingbird, belted kingfisher, flicker, red-headed woodpecker, phoebe, alder flycatcher, least flycatcher, rough-winged swallow, crow, house wren, catbird, brown thrasher, robin, bluebird, starling, white-eyed vireo, warbling vireo, blue-winged warbler, yellow warbler, chestnut-sided warbler, yellow-throat, Baltimore oriole, cardinal, rose-breasted grosbeak, indigo bunting, purple finch, goldfinch, towhee, vesper sparrow, chipping sparrow, field sparrow, and song sparrow. The cowbird was mentioned in nearly all reports, but seldom were figures determined on number present so this species has been omitted from the compilation. Perhaps the elimination of some of the above species seems arbitrary. The presence of the house wren throughout the 55-acre forest near Urbana, Illinois, has already been noted (Table 17). Towhees and cardinals, although usually forest-edge species, may sometimes occur through a forest where openings or thickets have been naturally made by trees being blown over or by other disturbance. However, such openings are "wounds" in the community structure, and since they occur to such a varying extent in different sample plots, it seems best to eliminate them altogether.

No census reported was without at least a few forest-edge species, because all plots bordered on open areas. In order to determine the influence of their presence on the density of the forest-interior birds Table 19 was worked out. Here the various censuses are arranged according to the percentage of the total population that was made up of forest-edge birds. This varied from only 4 percent to as much as 84 percent. It will be noted at once that the density of forest-interior birds fluctuated at random around 200 pairs per 100 acres in the first eight reports where the forest-edge birds did not exceed 38 percent of the total population, but at percentages above this mark the density of forest-interior birds decreased rapidly. One of the two areas with 38 percent forest-edge birds had a low density of forest-interior birds. Although the other area, No. 6, is included in the final summary (Table 20), because the density of forest-interior species is about average, one may say that a census is very likely not to show the true density of forest-interior birds if forest-edge birds constitute more than one-third of the total population. These latter reports are not thus included in the compilation.

TABLE 19. Relation of relative density of forest-edge birds to density of forest-interior birds.

Area[1]	Size in acres	Per cent forest-edge birds of total population	Number pairs forest-interior birds per 100 acres (40 hectares)
4.........	50	4	218
8.........	65	6	192
5.........	55	8	194
7.........	30	9	288
1.........	24	15	208
3.........	35	20	256
2.........	20	22	265
6.........	14	38	195
Cleveland, O......	26	38	103
Ithaca, N. Y......	25	41	170
Derby, O.........	35	41	65
Tulsa, Okla.......	34	42	96
Milwaukee, Wis...	13	44	63
Urbana, Ill.[2].....	55	66	61
Columbus, O......	27	84	60

[1]For location and description of numbered areas see pages 97-98.
[2]The data for Trelease Woods are here recalculated with the house wren and indigo bunting being included with the forest-edge species.

Although large areas of forests tend to have lower percentage of forest-edge species, size is not the only factor involved. Doubtlessly the amount of exposure to open country around the edge is important. The Urbana, Illinois, area (Trelease Woods), although the second largest censused, is bordered on all four sides by open farmland so that the infiltration of forest-edge species, like the house wren and indigo bunting, is more highly developed than in other areas of smaller size. On the other hand, areas 2 and 6, although small, are good samples as they have small edge exposure to open country.

The explanation for the reduction in forest-interior birds when greater numbers of forest-edge birds are present is one of interest and requires further study. There could be actual competition, either directly or indirectly, between these two groups for territory and a share of the carrying capacity of the forest or the larger percentage of forest-edge species may simply indicate that the community or habitat is no longer a true forest one and is changed in various ways that are less favorable for forest birds.

Eight areas were finally selected to combine into a composite picture of the avian population in the mature deciduous forest climax community (Table 20). The average population of each area is given when censuses cover more than one year. Description of these areas follows: Area 1 is near Shephardstown, West Virginia, and the single year's census was taken by S. K. Dandridge. Oaks of several species were dominant in the forest but there were also hickory, white and Virginia pine. There had been no cutting or grazing in the area for the last 60 years and the forest-edge was mostly limited to one corner.

Area 2 is located near Pamplin, Va., and a census for one year was obtained by Morton Marshall, Jr. This is an upland forest in which oaks and tulip trees dominate. The forest crown is somewhat open and a dirt road runs through the center of the area. The plot is surrounded on three sides by forest and on one side by farmland.

Area 3 lies near Yonkers, N. Y., and censuses over 5 years were obtained by J. J. Hickey and J. L. Bull, Jr. The forest is one of mixed hardwoods, and 5 acres were burned over in 1925 and 1933. There is a picnic area of one acre and a little over a mile of edge exposed to a reservoir, an orchard, a pasture, and shrubby growth.

Area 4 is one with oak-hickory forest alternating on the ridges and ravines with beech-maple forest. There is good undergrowth and the one year census was taken by Harold E. Wallin. The area is located near Cleveland, Ohio.

Area 5, near Youngstown, Ohio, is a wet lowland forest dominated by beech and sugar maple. The forest is ungrazed, with no open places, and only 0.4 mile exposed edge. Censuses have been taken over three years by E. O. Mellinger.

Area 6 lies near Wellington, Ohio, and is flat with a stream crossing it. It has an edge exposed to shrubby and swampy fields. Beech and sugar maple dominate. Censuses have been taken over 4 years by Belle L. Clisby.

Area 7, near Cleveland, Ohio, has been censused over 3 years by Vera Carrothers and Margaret E. Morse. It is a beech-maple forest, with open spaces due to cutting, other woods on one side, fields on two sides, and a highway with woods beyond on the fourth side.

Area 8 is an upland beech-maple forest with some hemlock along one edge. Black-throated green warblers found associated with these evergreens are here omitted from the census. Only one corner of the area is exposed to a grassy field and there is continuous forest in the other directions. A. B. Williams has censused this area for the last 10 years.

TABLE 20. Breeding birds (number of pairs) in mature relatively undisturbed climax deciduous forest.

Area number	1.	2.	3.	4.	5.	6.	7.	8.	Total	Number per 100 acres (40 hectares)
Type of forest	Oak	Oak-Tulip	Oak-Maple-Beech	Oak-Hickory with Beech-Maple	Beech-Maple	Beech-Maple	Beech-Maple	Beech-Maple		
Locality	West Virginia	Virginia	New York	Northern Ohio	Eastern Ohio	Northern Ohio	Northern Ohio	Northern Ohio		
Years' record	1	1	5	1	3	4	3	10		
Number of acres	24	20	35	50	55	14	30	65	293	...
Ruffed Grouse	0	0	0	1.0	0	0	0.3	0.1	1.4	0.5
Woodcock	0	0	0.2	0	0	0	0.3	0	0.5	0.2
Yellow-billed Cuckoo	1.0	2.0	0	0	0.3	0	0	0.2	3.5	1.2
Great Horned Owl	0	0	0	0	1.0	0.5	0	0	1.5	0.5
Barred Owl	1.0	1.0	0	0	1.0	0	0.7	1.0	4.7	1.6
Saw-whet Owl	0	0	0	0	0.3	0	0	0	0.3	0.1
Whip-poor-will	1.0	3.0	0	0	0	0	0	0	4.0	1.4
Pileated Woodpecker	0	1.0	0	0	0.7	0	0	0.1	1.8	0.6
Red-bellied Woodpecker	0	0	0	0	1.3	1.0	0	0.2	2.5	0.9
Hairy Woodpecker	0	1.0	0.2	1.0	1.7	0	1.7	2.5	8.1	2.8
Downy Woodpecker	0	1.0	2.0	2.0	2.7	2.2	3.3	3.1	16.3	5.6
Crested Flycatcher	9.0	1.0	2.2	2.0	3.0	1.8	1.7	1.6	22.3	7.6
Acadian Flycatcher	0	0	0	2.0	7.7	1.5	3.0	5.1	19.3	6.6
Wood Pewee	4.0	1.0	0.8	7.0	8.7	3.0	3.7	6.2	34.4	11.7
Blue Jay	0	1.0	0.2	0	2.3	0.5	0.3	0.4	4.7	1.6
Black-capped Chicadee	0	0	0.4	4.0	1.0	0	5.0	3.1	18.5	6.3
Carolina Chickadee	3.0	2.0	0	0	0	0	0	0		
Tufted Titmouse	2.0	2.0	0	5.0	7.0	3.5	3.0	5.7	28.2	9.6
White-breasted Nuthatch	1.0	2.0	1.0	2.0	2.7	1.8	1.7	3.2	15.4	5.3
Carolina Wren	1.0	0	0	0	0	0	0	0.1	1.1	0.4
Wood Thrush	5.0	5.0	0.2	8.0	6.3	1.0	6.7	14.0	46.2	15.8
Veery	0	0	9.6	0	0	0	3.0	0	12.6	4.3
Blue-gray Gnatcatcher	0	1.0	0	0	0.3	0.8	0	0	2.1	0.7
Yellow-throated Vireo	0	0	2.8	7.0	1.7	1.2	1.3	2.4	16.4	5.6
Red-eyed Vireo	11.0	11.0	15.0	13.0	13.0	2.2	12.3	25.1	102.6	35.0
Black and White Warbler	0	2.0	3.0	0	0	0	0	0	5.0	1.7
Worm-eating Warbler	2.0	0	9.0	0	0	0	0	0	11.0	3.8
Cerulean Warbler	0	0	0	10.0	8.0	1.2	3.3	1.2	23.7	8.1
Oven-bird	6.0	7.0	18.6	27.0	19.3	1.8	16.3	16.4	112.4	38.4
Louisiana Water-thrush	1.0	0	0	2.0	0	1.0	0.3	1.9	6.2	2.1
Kentucky Warbler	0	0	0.4	0	0	0	0	0	0.4	0.1
Hooded Warbler	0	5.0	3.2	2.0	0	0.5	4.7	12.9	28.3	9.7
Redstart	0	2.0	21.0	11.0	10.7	0.8	12.0	12.3	69.8	23.8
Scarlet Tanager	2.0	0	0.4	3.0	6.0	1.0	1.7	6.1	22.2	7.6
Summer Tanager	0	2.0	0	0	0	0	0	0		
Total	50.0	53.0	90.2	109.0	106.7	27.3	86.3	124.9	647.4	
Number per 100 acres	208.0	265.0	256.0	218.0	194.0	195.0	288.0	192.0	221.0	221.0

There has been no recent cutting or grazing here, although there are foot and horse trails and a trail-side museum within the boundaries of the area censused.

A study of Table 20 shows considerable similarity between the various censuses, and so they need not be discussed individually. Elton (1935) found similar agreement in the species composition of woodland birds in different types of forest in Europe. In general the constitution of the bird population is conspicuous for its 4 species of Picidae, 3 species of Tyrannidae, 3 Paridae, 2 Turdidae, 2 Vireonidae, 8 Compsothlypidae, 2 Thraupidae, and the entire lack of Fringillidae. In descending order of abundance the leading 7 species rank as follows: oven-bird, red-eyed vireo, redstart, wood thrush, wood pewee, hooded warbler, and tufted titmouse. The three species of owls are indicated here to be represented by a little more than two pairs per 100 acres. Probably this is high as several individual reports indicated that the owls often went outside the limits of the census area for feeding purposes. Probably one pair per 100 acres would more clearly represent their usual density. The total population of all species may be taken as 220 pairs per 100 acres, which is equal to 2.2 pairs per acre and 5.5 pairs per hectare. Variation between the total population on the eight areas is relatively small, the extremes being 192 and 288 per 100 acres. The standard deviation is ± 35, and the coefficient of variation equals 16 percent. There would be considerable interest in making similar compilations for other major ecolog-

ical communities, but at the present time there is a dearth of suitable data.

DISCUSSION

In the progress of ornithological research, especially in respect to field studies, various steps or stages may be recognized. First came exploration, with the identification, description, and naming of species and their races. Although not complete, for North America north of Mexico it is relatively far advanced. The next step was the working out of distributional ranges at all seasons of the year. This also is fairly well known for most species in North America. The third step in this progress is the determination of the abundance of each species in all parts of its range. Much work has been done on this problem in a general way but the study needs to be placed on a more exact quantitative basis. It is with this aspect that the present paper is most concerned. More or less coinciding with this development is the next stage wherein each species is designated to its proper ecological community or communities with a measurement of its abundance in each community. A fifth stage may be added which involves analysis of factors controlling the species' occurrence within particular local communities as well as factors controlling its geographic distribution. This involves physiological and morphological research as well as detailed behavior and life-history studies.

The value of a more exact determination of the abundance of birds is obvious. For some purposes it is sufficient to know only the abundance of different species in relation to one another or of the same species under different conditions. For other purposes it is desirable to know the absolute population of each species as accurately as possible. This is important in wildlife management for making inventories of game animals, testing the effect of various management processes, and regulating the harvest by sportsmen. Measurement of actual populations is required in ecological studies dealing with the relations of various species within the community. For example, in working out food-chains, it is not sufficient to know the relative abundance of the various species of birds amongst themselves. One needs information on the actual number of birds to compare with the actual size of the population of mammals, insects, and other invertebrates upon which they prey or are preyed upon and with the volume of foliage or seeds upon which they ultimately depend. For these reasons, population studies should be put upon an absolute quantitative basis wherever possible. Probably studies of the abundance of birds on the relative basis will eventually have to be done over, because such studies have only a limited application to problems that are coming to be more and more important.

Measurement of the size of animal populations is a full-time job and should be treated as a worthy end in itself. Doubtlessly the reason the abundance of birds has been and is now often expressed only in relative terms is that the determination of abundance has been incidental to other objectives and the observer has not considered it worthwhile or at least has not taken the time to obtain the additional information necessary.

In any large scale investigation of animal populations or where the results are to be subject to various statistical manipulations, a trained statistician should be consulted before the project is begun. Often there is a waste of time and effort or the investigation must be repeated or the results are not fully usable because certain variables were overlooked which a statistician, brought into consultation when the undertaking was being planned, could have pointed out. This point received some emphasis in a symposium on animal populations held jointly by the American Statistical Association and the Ecological Society of America in Chicago on December 26, 1940.

It is very unfortunate that lists of birds seen by amateurs and professionals alike on trips designed to record as many species as possible are so difficult of statistical manipulation. These lists should be a mine of information on bird populations as there must be thousands of such lists available for all parts of the world. How their utilization may be effected still needs to be solved.

Certain field workers have expressed the philosophy that only approximate accuracy needs to be attained in population studies of this sort, as perfect accuracy is not required to produce valuable results nor is it worth the time and energy involved. The trouble with this is that the degree of accuracy will vary widely in studies performed by different individuals, by the same individual at different times, or when applied to different groups of animals. Therefore the results of such studies are not comparable with any degree of confidence. Far better it seems to strive for the ultimate degree of accuracy with the development of the best practicable methods, and if this ultimate accuracy cannot be attained, then measure the amount of error involved. This will permit reliable comparisons of different censuses and will stimulate further improvements in method.

SUMMARY AND CONCLUSIONS

1. Following an early concentration on exploration and taxonomy in this country measurement of bird populations began to be undertaken in earnest at the beginning of the present century. This measurement received added impetus and importance with the development of the modern program of wildlife management beginning about 1930. There is considerable interest in measuring bird populations in the British Commonwealth, in Finland, Germany, Russia, and to a lesser extent in France.

2. Abundance of birds may be measured in relative terms or as actual populations. Although determination of relative abundance is sufficient for some purposes, it is more limited in its use and application than determination of actual populations, and the use

and improvement of true census methods is encouraged.

3. Relative abundance has been commonly measured as percentage of days or trips on which the species was recorded, number of individuals observed per trip or per unit of time (hour) or per unit of distance (mile), or by a combination of these methods. All these methods have serious imperfections unless corrections are made for difference in conspicuousness of the various species and for the relative amount of observations made in different communities (habitats).

4. The use of several of these methods is illustrated with data from northern Ohio (Tables 1-8). Differences in the conspicuousness of various species were measured by the average distance at which their presence was first observed (Table 9). The relative abundance of 22 species in northern Ohio during the winter months is presented (Table 10) after correcting for their differences in conspicuousness and community occurrence. These methods were found more applicable during the wintering than during the breeding season.

5. Data on the number of bob-white in Ohio in early winter for the period, 1908 to 1942 inclusive (Fig. 1), suggest yearly fluctuations of a rhythmical nature with high populations having been attained in 1911 or 1912, 1923 or 1924, and 1935, and low populations in 1909 (?), 1915, 1928 or 1929, and 1940.

6. Analysis of the breeding population curve for the house wren for the period, 1915 to 1940 inclusive, shows marked low points about 1917, in 1926, and in 1940 (Fig. 2). Superimposed on these major fluctuations is a possible 3-4-year variation. Major fluctuations in size of the population are correlated with temperature variations during the wintering season above and below a critical temperature of 56° F. (13° C.). Immature birds appear more sensitive and responsive to environmental changes than birds of two years age or older.

7. In species with more than one brood per year, there may be additions or substractions to the population between breeding periods that are difficult to detect unless the birds are individually identified by banding or marking. Such changes should be considered in computing population densities. In the house wren they amount to 23 percent of the total population. In considering population densities, one should keep in mind that in addition to the breeding birds, there may be a substantial non-breeding population that is difficult to measure.

8. In the house wren, about 9 percent of the singing males do not secure mates for nesting at any time during the season.

9. With the use of the strip census method in the vicinity of Reelfoot Lake in western Tennessee, populations of birds during the spring migration period was found to vary from 6 per 100 acres (40 hectares) on open water in the Mississippi River to 390-640 per 100 acres in mid-seral forest communities, and back to 280 per 100 acres in the climax beech forest.

10. In censusing total breeding populations of all species, sample plots of 50 acres (20 hectares) for forest communities and 75 acres (30 hectares) for open fields or grasslands are recommended as convenient for one person to cover efficiently in a day. Large areas may be covered successfully for wintering populations. Basing population densities upon the finding of nests alone is inadequate, especially in forest communities, and the most successful practicable method so far developed is the approximate mapping of territories as they become established throughout the season. For accurate figures on total populations during the breeding season, five complete surveys are desirable and these should be distributed from April to July, inclusive.

11. The number of nests that occurred yearly on a 15-acre (6 hectares) country estate in northern Ohio is given for the period, 1925 to 1939 inclusive, for 10 species (Table 15). Fluctuations in number of nests from year to year appeared for most species to have only a local significance.

12. The breeding population in a 55-acre (22 hectares) oak-maple woods in central Illinois is given for 11 years between 1927 and 1943 (Table 17). During this period the red-eyed vireo and crested flycatcher increased in abundance, the starling and house wren invaded the area in large numbers, while the red-headed woodpecker, cardinal, and wood thrush decreased. Censuses in the same area for 14 winters beginning in 1924-25 show that the downy and red-bellied woodpeckers increased in abundance, the starling invaded the area, the cardinal decreased, while the other species remained fairly constant (Table 18).

13. Computation of population densities require separation of forest-edge birds from forest-interior ones. The density of forest-interior species may be greatly reduced during the breeding season when the percentage of forest-edge species equals more than one-third of the total population. Density is best expressed as number of birds (non-breeding season) or potential pairs (breeding season) per 40 hectares (100 acres). When the forest-edge is narrow or of uncertain width, density may be expressed as number per kilometer (0.62 mile).

14. Bird censuses should be restricted to single biotic communities. These communities may be recognized and designated primarily by the vegetation type or life-form of the dominant plants and secondarily by the dominant plant species. The community to be complete should include the entire area covered by the activities of the animals concerned.

15. An analysis is made of the species composition and average number of individuals of each species making up the avian population in mature, relatively undisturbed, climax forests of the deciduous forest biome (Table 20). The total population of forest-interior species amounts to 220 pairs per 100 acres (40 hectares).

LITERATURE CITED

Alexander, W. B. 1942. The index of heron population, 1941. Brit. Birds **35:** 210-213.

Allan, Philip F., & Palmer R. Sime. 1943. A hawk census on Texas highways. Wils. Bull. **55:** 29-39.

Allen, Durward L. 1938. Ecological studies on the vertebrate fauna of a 500-acre farm in Kalamazoo County, Michigan. Ecol. Mono. **8:** 347-436.

1942. A pheasant inventory method based upon kill records and sex ratios. Trans. 7th No. Amer. Wildlife Conf. 329-333.

Allen, Robert P. 1937. Black-crowned night heron colonies on Long Island. Proc. Linn. Soc. N. Y. No. **49:** 43-51.

Baldwin, S. Prentiss. 1919. Bird-banding by means of systematic trapping. Abst. Proc. Linn. Soc. N. Y. No. **31:** 23-56.

Baldwin, S. Prentiss, S. Charles Kendeigh, & Roscoe W. Franks. 1932. The protection of hawks and owls in Ohio. Ohio Jour. Sci. **32:** 403-424.

Beecher, William J. 1942. Nesting birds and the vegetation substrate. Chicago Ornith. Soc., Chicago 1-69.

Bell, W. B. 1937. Methods in wildlife censuses. Jour. Amer. Statist. Assoc. **32:** 537-542.

Bennett, Logan J., & George O. Hendrickson. 1938. Censusing the ringneck pheasant in Iowa. Trans. 3rd No. Amer. Wildlife Conf. 719-723.

1938a. Censusing quail in early fall. Jour. Wildlife Manag. **2:** 169-171.

Bennitt, Rudolf, & Werner O. Nagel. 1937. A survey of the resident game and fur-bearers of Missouri. Univ. Mo. Studies **12:** 1-215.

Bergman, G. 1939. Untersuchungen über die Nistvogelfauna in einem Schärengebiet westlich von Helsingfors. Acta Zoologica Fennica **23:** 1-134.

Blake, Irving Hill. 1926. A comparison of the animal communities of coniferous and deciduous forests. Ill. Biol. Mon. **10:** 1-149.

Boyd, A. W. 1933. Notes on the swallow and size of broods in Cheshire. Brit. Birds **26:** 255-256.

1935. Report on the swallow enquiry, 1934. Brit. Birds **29:** 3-21.

1936. Report on the swallow enquiry, 1935. Brit. Birds **30:** 98-116.

Braun, E. Lucy. 1942. Forests of the Cumberland Mountains. Ecol. Mono. **12:** 413-447.

Braun, Howard, & Grover Keplinger, Jr. 1938. The spring, 1938, warbler migration. Inland Bird-Banding News (mimeographed) **10:** 3.

Braun-Blanquet, Josias. 1932. Plant sociology. (Translated by George D. Fuller anl Henry S. Conrad.) New York i-xviii, 1-439.

(Bray, Robert S.) 1938. Wildlife census methods applicable to National Parks and Monuments. Nat. Pk. Serv., Dept. Int. 1-20 (mimeographed).

Breckenridge, W. J. 1935. A bird census method. Wils. Bull. **47:** 195-197.

Burns, Frank L. 1901. Further suggestions for the taking of a bird census. Wils. Bull. **8:** 52-53.

1901. A sectional bird census. Wils. Bull. **8:** 84-103.

1907. Alexander Wilson in bird census work. Wils. Bul. **19:** 100-102.

1914. A second sectional bird census. Bird-Lore **17:** 109-111.

Chapman, Floyd B. 1937. A quantitative study of the breeding birds of Nile Township, Scioto County, Ohio. Ohio Wildlife Res. Sta. Release No. 40 (mimeographed).

Chapman, W. M. M. 1939. The bird population on an Oxfordshire farm. Journ. Animal Ecol. **8:** 286-299.

Chappellier, A., & Dalmon, J. 1933. Les Dortoirs de Corbeaux. L'Oiseau et la Rev. franc. d'Ornith. No. **2:** 379-385.

Chappellier, A. 1934. Recherche des Points et Voies de Penetration en France des Corbeaux Migrateurs. Revue des Eaux et Forets 94-113.

Chitty, Dennis, & Charles Elton. 1937. Canadian Arctic wildlife enquiry, 1935-36. Journ. Animal Ecol. **6:** 368-385.

Chitty, Dennis, & Mary Nicholson. 1942. Canadian Arctic wildlife enquiry, 1940-41. Journ. Animal Ecol. **11:** 270-287.

Cleland, J. Burton. 1918. The birds of the Pilliga Scrub, New South Wales. Emu **18:** 272-285.

1922. A method of taking a bird census. Emu **22:** 18-23.

Clements, Frederic E., & Victor E. Shelford. 1939. Bio-Ecology. New York, i-vii, 1-425.

Colquhoun, M. K. 1940. The density of woodland birds determined by the sample count method. Journ. Animal Ecol. **9:** 53-67.

1941. Visual and auditory conspicuousness in a woodland bird community: a quantitative analysis. Proc. Zool. Soc. London, Sec. A, **110:** 129-148.

1941. The birds of Savernake Forest, Wiltshire. Journ. Animal Ecol. **10:** 25-34.

Colquhoun, M. K., & Averil Morley. 1941. The density of downland birds. Journ. Animal Ecol. **10:** 35-46.

Cooke, W. W. 1915. Preliminary census of birds in the United States. Bull. U. S. Dept. Agr. No. **187:** 1-11.

1916. Second annual report of bird counts in the United States, with discussion of results. Bull. U. S. Dept. Agr. No. **396:** 1-20.

Cooke, May Thatcher. 1923. Report on bird censuses in the United States 1916 to 1920. U. S. Dept. Agr. Bull. **1165:** 1-34.

1927. The purpose of bird censuses and how to take them. U. S. Dept. Agr. Circ. **261:** 1-4.

Cramp, S., & J. H. Ward. 1934. A census of house martins and swallows near Manchester, 1933. Journ. Animal Ecol. **3:** 1-7.

1936. The rookeries of South Manchester and district. Journ. Animal Ecol. **5:** 351-355.

Dambach, Charles A. 1941. The effect of land-use adjustments on wildlife populations in the Ohio valley region. Trans. 5th No. Amer. Wildlife Conf. **1941:** 331-337.

Dambach, Charles A., & E. E. Good. 1940. The effect of certain land use practices on populations of breeding birds in southwestern Ohio. Journ. Wildlife Manag. **4:** 63-76.

Davis, David E. 1942. A new census method applied to Cuban birds. Ecol. **23:** 370-376.

Davison, Verne E. 1940. An 8-year census of lesser prairie chickens. Journ. Wildlife Manag. **4:** 55-62.

Dawson, W. L. 1897. Committee of geographical distribution of birds. Wils. Ornith. Chapter, General Notes, Bull. **14:** 31-33.

1898. Committee on geographical distribution. Wils. Ornith. Chapter, General Notes, Bull. **19:** 28-29.

Dice, Lee R. 1930. Methods of indicating relative abundance of birds. Auk **47:** 22-24.

De Lury, Ralph. 1934. Fluctuations in the numbers of birds revealed by bird-banding. East. Bird-Banding Quart. **1:** 6.

Douglass, Donald W. 1942. A prairie chicken booming grounds survey in central Michigan. Wils. Bull. **54**: 171-172.

Eaton, Warren F. 1934. Eighteen years of Wyanokie (1916-1933). Abst. Proc. Linn. Soc. N. Y., Nos. **43, 44**: 14-26.

1936. Some notes on the 1935 season, especially on the raptorial birds of the northeast. Nat. Assoc. Aud. Soc., Circ. **24**: 1-16.

Elton, Charles. 1935. A reconnaissance of woodland bird communities in England and Wales. Journ. Animal Ecol. **4**: 127-136.

Emlen, John T., Jr. 1938. Midwinter distribution of the American crow in New York State. Ecol. **19**: 264-275.

1940. The midwinter distribution of the crow in California. Condor **42**: 287-294.

Errington, Paul L. 1933. The wintering of the Wisconsin bob-white. Trans. Wis. Acad. Sci. and Let. **28**: 1-35.

1941. An eight-winter study of central Iowa bobwhites. Wils. Bull. **53**: 85-101.

Errington, Paul L., & F. N. Hamerstrom, Jr. 1936. The northern bob-white's winter territory. Iowa St. College, Agr. Exp. Sta. Res. Bull. **201**: 301-443.

Fish and Wildlife Service, U. S. Department of Interior. 1941. The status of migratory game birds, 1940-41. Wildlife Leaflet **196**: 1-28.

Fisher, James. 1939. Birds as animals. Toronto, i-xviii, 1-281.

Fisher, James, & L. S. V. Venables. 1938. Gannets (Sula bassana) on Noss, Shetland, with an analysis of the rate of increase of this species. Journ. Animal Ecol. **7**: 305-313.

Fisher, James, & H. G. Vevers. 1939. The world distribution and numbers of breeding gannets. Bull. Brit. Orn. Club **40**: 39-41.

Fisher, James, & George Waterson. 1941. The breeding distribution, history and population of the fulmar (Fulmarus glacialis) in the British Isles. Journ. Animal Ecol. **10**: 204-272.

Fisher, Lee William. 1939. Studies of the eastern ruffed grouse in Michigan (Bonasa umbellus umbellus) Agr. Exp. Sta., Mich. St. College, Tech. Bull. **166**: 1-46.

Forbes, Stephen A. 1907. An ornithological cross-section of Illinois in autumn. Bull. Ill. St. Lab. Nat. Hist., **7**: 305-332.

1913. The midsummer bird life of Illinois: a statistical study. Bull. Ill. St. Lab. Nat. Hist., **9**: 373-385.

Forbes, Stephen A., & Alfred Gross. 1921. The orchard birds of an Illinois summer. Bull. Ill. Nat. Hist. Survey, **14**: 1-8.

1922. The numbers and local distribution in summer of Illinois land birds of the open country. Bull. Ill. Nat. Hist. Survey, **14**: 187-218.

1923. On the numbers and local distribution of Illinois land birds of the open country in winter, spring, and fall. Bull. Ill. Nat. Hist. Survey, **14**: 397-453.

Forbush, Edward Howe. 1905. Special report on the decrease of certain birds, and its causes, with suggestions for bird protection. Mass. St. Bd. Agr., 52nd Annual Rep. 429-543.

1917. Tenth annual report of State Ornithologist, Mass. 14-22.

1923. Report of the division of ornithology, 1922. Dept. Agr. Publ. **126**: 1-23.

Ganier, Albert F. 1938. The relative abundance of winter birds at Nashville. Migrant **9**: 89-93.

Glading, Ben. 1941. Valley quail census methods and populations at the San Joaquin Experimental Range. Calif. Fish and Game **27**: 33-38.

Goddard, T. Russell. 1935. A census of short-eared owls (Asio f. flammeus) at Newcastleton, Roxburghshire, 1934. Journ. Animal Ecol. **4**: 113-118.

1935. A census of short-eared owls (Asio f. flammeus) at Newcastleton, Roxburghshire, 1935. Journ. Animal Ecol. **4**: 289-290.

Graham, Samuel A. 1940. The intersection method of counting animals. Journ. Wildlife Manag. **4**: 313-314.

Griscom, Ludlow. 1942. The changing seasons. Audubon Mag. 44, Sect. **1**: 318-319; Sect. **2**: 2-15.

Granit, Olof. 1938. Versuch zur quantitativen Untersuchung der Vogelfauna einer Fjeldgegend in Nordfinnland. Ornis Fennica **15**: 53-65. (Bird-Banding 10, **1939**: 53.)

Grant, Martin L., & Dorothy S. 1943. The first annual Iowa spring bird census. Iowa Bird Life **13**: 41-48.

Green, R. G. 1938. Grouse populations, Minnesota wildlife disease investigation. Dept. Bact., U. of Minn. 74-76 (mimeographed).

Grinnell, Joseph, & Tracy Irwin Storer. 1924. Animal life in the Yosemite. Univ. Calif. Press, Berkeley i-xviii, 1-752.

Grosvenor, G. H. 1916. The world's record for density of bird population. Bird-Lore **18**: 77.

Harrisson, T. H., & H. G. Hurrell. 1933. Numerical fluctuations of the great black-backed gull (Larus marinus Linn.) in England and Wales. Proc. Zool. Soc. London 191-209.

Harrisson, T. H., & P. A. D. Hollom. 1933. The great crested grebe enquiry (1931) Scotland. Brit. Birds **26**: 286-291.

Harrisson, T. H., & D. Lack. 1934. The breeding birds of St. Kilda. Scottish Nat. 59-60.

Hawkins, Arthur S., & Frank C. Bellrose. 1939. The duck flight and kill along the Illinois River during the fall of 1938. Amer. Wildlife **28**: 178-186.

Hickey, J. J. 1937. Report of the field work committee, 1936-37. Abst. Proc. Linn. Soc. N. Y., No. **49**: 73-83.

1943. A guide to bird watching. New York, i-xiv, 1-262.

Hickey, Margaret B. 1942. Audubon Magazine's sixth breeding-bird census. Audubon Mag. 44, Sect. **2**: 16-32.

Hicks, Lawrence E. 1935. A ten-year study of a bird population in central Ohio. Amer. Midl. Nat. **16**: 177-186.

1937. Breeding birds of unglaciated Ohio. Cardinal **4**: 125-141.

Hicks, Lawrence E., & Floyd B. Chapman. 1933. A statistical survey of Ohio winter bird life. Ohio Journ. Sci. **33**: 135-150.

Hicks, Lawrence E., & Charles A. Dambach. 1936. A statistical survey of the winter bird life of southeastern Ohio, Muskingum County. Wils. Bull. **48**: 273-275.

Hollom, P. A. D. 1933. The great-crested grebe in the London area. London Nat. for 1932: 51-56.

1936. Report on great crested grebe sample count, 1935. Brit. Birds **30**: 138-158.

1940. Report on the 1938 survey of black-headed gull colonies. Brit. Birds **33**: 202-221, 230-244.

Hornberger, F. 1939. Zehn ostpreussische Storch-Zählungen. Ornith. Monatsb. **47**: 166-170.

Hosley, N. W., R. I. Ashman, W. E. Bradder, P. D. Dalke, & A. E. Moss. 1936. Forest wildlife census methods applicable to New England conditions. Journ. Forest. **34**: 467-471.

Jones, Lynds. 1898. The bird census. Wils. Orn. Chapter, General Notes, Bull. **18**: 5-9.

1901. A suggestion for work. Wils. Bull. **8**: 49-52.

1902. A New Year horizon for all. Wils. Bull. **9**: 133-134.

1903. A May day horizon. Wils. Bull. **10**: 31.

1904. July Fourth censo-horizons. Wils. Bull. **11**: 76-80.

1916. The May bird census for 1916. Wils. Bull. **23**: 143-147.

Kalela, Olavi. 1938. Über die regionale Verteilung der Brutvogelfauna im Flussgebiet des Kokemäenjoki. Annales Zoologici Soc. Zool.-Bot. Fennicae Vanamo, **5**: 1-291.

Kashkarov, D. N. 1927. The quantitative method in the field study of vertebrate fauna and analysis of the data obtained. Acta Universitatis Asiae Mediae, Ser. 8a. Fasc. **1**: 1-24 (in Russian with English summary).

Kendeigh, S. Charles. 1933. Abundance and conservation of the bob-white in Ohio. Ohio Journ. Sci. **33**: 1-18.

1934. The role of environment in the life of birds. Ecol. Mono. **4**: 299-417.

1941. Birds of a prairie community. Condor **43**: 165-174.

1941a. Territorial and mating behavior of the house wren. Ill. Biol. Mono. **18**: 1-120.

Kendeigh, S. Charles, & S. Prentiss Baldwin. 1937. Factors affecting yearly abundance of passerine birds. Ecol. Mono. **7**: 91-124.

Klockars, B. 1936. Attempt at a quantitative study of winter bird population. Ornis Fennica **13**: 139-147.

Lack, David. 1935. The breeding bird population of British heaths and moorland. (Together with an account of a census over seven years on Skokholm, Pembrokeshire by R. M. Lockley.) Journ. Animal Ecol. **4**: 43-57.

1937. A review of bird census work and bird population problems. Ibis, Ser. 14, **1**: 369-395.

1940. The behaviour of the robin. Population changes over four years. Ibis, Ser. 14, **4**: 299-324.

1942. Ecological features of the bird faunas of British small islands. Journ. Animal Ecol. **11**: 9-36.

Lack, David, & L. S. V. Venables. 1937. The heathland birds of South Haven Peninsula, Studland Heath, Dorset. Journ. Animal Ecol. **6**: 62-72.

1939. The habitat distribution of British birds. Journ. Animal Ecol. **8**: 39-71.

Lay, Daniel W. 1938. How valuable are woodland clearings to birdlife? Wils. Bull. **50**: 254-256.

1940. Bob-white populations as affected by woodland management in eastern Texas. Tex. Agr. Exp. Sta., Bull. **592**: 1-37.

Leopold, Aldo. 1930. The decline of the jacksnipe in southern Wisconsin. Wils. Bull. **42**: 183-190.

1931. Report on a game survey of the North Central States. Madison, Wisconsin, 1-299.

1942. A raptor tally in the northwest. Condor **44**: 37-38.

Lehmann, Valgene W. 1941. Attwater's prairie chicken, its life history and management. No. Amer. Fauna 57, Fish and Wildlife Service 1-63.

Lewis, Harrison F. 1931. Five years' progress in the bird sanctuaries of the north shore of the Gulf of St. Lawrence. Canadian Field-Nat. **45**: 73-78.

1942. Fourth census of non-passerine birds in the bird sanctuaries of the north shore of the Gulf of St. Lawrence. Canadian Field-Nat. **56**: 5-8.

Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. U. S. Dept. Agr., Circ. **118**: 1-4.

Linsdale, Jean M. 1924. A method of showing relative frequency of occurrence of birds. Condor **30**: 180-184.

1932. Frequency of occurrence of birds in Yosemite Valley, California. Condor **34**: 221-226.

1936. Frequency of occurrence of summer birds in northern Michigan. Wils. Bull. **48**: 158-163.

Linsdale, Jean M., & Thomas L. Rodgers. 1937. Frequency of occurrence of birds in Alum Rock Park, Santa Clara County, California. Condor **39**: 108-111.

Lister, M. D. 1939. An account of the lapwing population of a Surrey farm. Brit. Birds **32**: 260-271.

Marples, B. J. 1934. The winter starling roosts of Great Britain, 1932-33. Journ. Animal Ecol. **3**: 187-203.

1935. The feeding grounds of rooks and other birds. Journ. Animal Ecol. **4**: 79-81.

Mason, C. R. 1936. Counting ducks from an airplane. Fla. Nat. **9**: 65-67 (fide Bray, 1938).

Mason, Edwin A. 1942. Relative abundance and sex ratios of warblers. Bird-Banding **13**: 13-18.

Maynard, Vera. 1936. The bird population of an area in Sussex. Journ. Animal Ecol. **5**: 312-318.

McClure, H. Elliott. 1939. Cooing activity and censusing of the mourning dove. Journ. Wildlife Manag. **3**: 323-328.

1942. Mourning dove production in southeastern Iowa. Auk **59**: 64-75.

Meylan's, O. 1934. Les Cèvennes et le Massif central. Contribution à l'étude avifaunistique d'une règion montagneuse. Arch. suisses d'Ornith. **1**: 113-140.

Middleton, A. D. 1934. Periodic fluctuations in British game populations. Journ. Animal Ecol. **3**: 231-249.

1935. Factors controlling the population of the partridge (Perdix perdix) in Great Britain. Proc. Zool. Soc. Lond. 795-815.

1935. The population of partridges (Perdix perdix) in 1933 and 1934 in Great Britain. Journ. Animal Ecol. **4**: 137-145.

1936. The population of partridges (Perdix perdix) in Great Britain during 1935. Journ. Animal Ecol. **5**: 252-261.

1937. The population of partridges (Perdix perdix) in Great Britain during 1936. Journ. Animal Ecol. **6**: 318-321.

Mitchell, M. 1938. The rook (Corvus frugilegus) population of northeast Denbighshire. Journ. Animal Ecol. **7**: 20-21.

Moffitt, James. 1943. Twelfth annual black brant census in California. Calif. Fish and Game **29**: 19-28.

More Game Birds in America. 1935. The 1935 international wild duck census. New York 1-79.

Moreau, R. E., & W. M. Moreau. 1931. The bird population of a settled valley in the West Usambaras, Tanganyika Territory. Journ. Ecol. **19**: 64-74.

Morrey, Salmon H., & R. M. Lockley. 1933. The Grassholm gannets: a survey and a census. Brit. Birds **27**: 142-152.

Murphy, Robert Cushman. 1925. Bird islands of Peru; the record of a sojourn on the west coast. New York. i-xx, 1-362.

Nauman, E. D. 1926. An Iowa bird census. Wils. Bull. **38:** 83-91.

Nice, Margaret M., & L. B. Nice. 1921. The roadside census. Wils. Bull. **38:** 113-123.

Nice, Margaret M. 1927. Seasonal fluctuations in bird life in central Oklahoma. Condor **29:** 144-149.
1929. Eight mile censuses in 1927. Condor **31:** 79.
1930. The technique of studying nesting song sparrows. Bird-Banding **1:** 177-181.
1934. A hawk census from Arizona to Massachusetts. Wils. Bull. **46:** 93-95.
1941. Spring and winter hawk censuses from Illinois to Oklahoma. Auk **58:** 403-405.
1941a. The role of territory in bird life. Amer. Midl. Nat. **26:** 441-487.

Nichols, John T. 1921. Estimated numbers of shore birds. Auk **38:** 110-112.
1937. Numbers of certain Long Island waterfowl from Bird-Lore's Christmas census. Bird-Lore **39:** 431-433.
1939. Seasonal starling numbers in suburban Long Island. Auk **56:** 478-479.

Nicholson, E. M. 1927. How birds live. London 1-139.
1928. Report on the British Birds census of heronies. Brit. Birds **22:** 270-323, 334-372.
1931. The art of bird-watching. London 1-218.

Nicholson, E. M., & J. Fisher. 1940. A bird census of St. Kilda, 1939. Brit. Birds **34:** 29-35.

Palmgren, Pontus. 1929. Kvantitative undersökningar över fågel-fauna i Finlands skogar. Det. 18. Skandinaviske Naturforskermøde, p. 55.
1930. Quantitative Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands mit besonderer Berücksichtigung Ålands. Acta Zoologica Fennica **7:** 1-219.
1931. Einige quantitative Vogelbestandsaufnahmen aus Muonio, Lappland. Ornis Fennica **3-4:** 73-84.
1933. Die Vogelbestände zweier Wäldchen, nebst Bemerkungen über die Brutreviertheorie und zur quantitativen Methodik bie Vogelbestandaufnahmen. Ornis Fennica **10:** 61-94.
1936. Über die Vogelfauna der Binnengewässer Ålands. Acta Zoologica Fennica **17:** 1-59.
1941. Oekologische Probleme der Ornithologie. Journ. f. Ornith. **89:** 103-123.

Perkins, E. H. 1914. Some results of Bird-Lore's Christmas bird censuses. Bird-Lore **16:** 13.

Pierce, Fred J. 1940. Winter birds of northeastern Iowa. Proc. Iowa Acad. Sci. **47:** 371-385.

Pitelka, Frank A. 1941. Distribution of birds in relation to major biotic communities. Amer. Midl. Nat. **25:** 113-137.
1942. High population of breeding birds within an artificial habitat. Ecology **44:** 172-174.

Price, M. P. 1935. Notes on population problems and territorial habits of chiff-chaffs and willow-warblers. Brit. Birds **29:** 158-166.
1935. Census of nightingales in Gloucestershire. Brit. Birds. **29:** 81-83.

Randall, Pierce E., & Logan J. Bennett. 1939. Censusing ringneck pheasants in Pennsylvania. 4th N. Amer. Wildlife Conf. 431-436.

Rodgers, Thomas L., & Charles G. Sibley. 1940. Frequency of occurrence of birds on the Berkeley campus, University of California. Condor **42:** 203-206.

Roebuck, A. 1933. A survey of the rooks in the Midlands. Brit. Birds **27:** 4-23.

Saunders, Aretas A. 1914. An ecological study of the breeding birds of an area near Choteau, Mont. Auk **31:** 200-210.
1936. Ecology of the birds of Quaker Run Valley, Allegany State Park, New York. N. Y. St. Mus. Hdbk. **16:** 1-174.
1938. Studies of breeding birds in the Allegany State Park. N. Y. St. Mus. Bull. **318:** 1-160.

Schiermann, Gottfried. 1930. Studien über Siedelungsdichte im Brutgebiet. Journ. für Ornith. **78:** 137-180.
1934. Studien über Siedlungsdichte im Brutgebiet. II. Der brandenburgische Kiefernwald. Journ. für Ornith. **82:** 455-486.

Schüz, Ernst. 1933. Der Bestand des Weissen Storchs (Ciconia c. ciconia) in Ostpreussen 1931. Verh. Ornith. Ges. Bay. **20:** 191-225.

Seeley, George M. 1937. The scarcity of small landbirds. Bird-Lore **39:** 463-464.

Serle, W., & D. Bryson. 1935. Distribution and number of the dipper on the N. and S. Esks (Midlothian). Brit. Birds **28:** 327-331.

Serventy, D. L. 1938. The relative abundance of birds. Emu **37:** 269-273.

Shaver, Jesse M. 1933. The influence of climatic and weather factors upon the numbers of birds on a depositing creek bank. Ecol. Mono. **3:** 535-597.

Shaver, Jesse M., & Compton Crook. 1934. The birds on the campus of George Peabody College for Teachers, Nashville, Tennessee. Jour. Tenn. Acad. Sci. **9:** 278-287; 1935, **10:** 77-82.

Shelford, Victor E. 1926. Naturalist's guide to the Americas. Baltimore i-xv: 1-761.

Smith, Frank. 1922. The European starling in Illinois. Trans. Ill. St. Acad. Sci. **15:** 185.

Southern, H. N. 1938. A survey of the vertebrate fauna of the Isle of May (Firth of Forth). Journ. Animal Ecol. **7:** 144-154.

Soveri, Jorma. 1940. Die Vogelfauna von Lammi, ihre regionale Vebreitung und Abhängigkeit von den ökologischen Faktoren. Acta Zool. Fenn. **27:** 1-176 (fide Bird-Banding 12, **1941:** 89-90).

Speirs, J. Murray. 1939. Fluctuations in numbers of birds in the Toronto region. Auk **56:** 411-419.

Stewart, Robert E. 1943. A comparative study of the breeding bird population of the Shenandoah Mountains, Virginia. Auk **60:** 388-396.

Stoner, Emerson A. 1934. Summary of a record of duck shooting on the Suisun Marsh. Condor **36:** 105-107.

Sundström, Kurt Erik. 1927. Ökologisch-geographische Studien über die Vogelfauna der gegend von Ekenäs. Acta Zool. Fenn. **3:** 1-170.

Tucker, B. W. 1935. The rookeries of Somerset. Proc. Somersetshire Archaeol. and Nat. Hist. Soc. **81:** 149-240.

Tuovinsen, A. 1936. The bird population of the island Nesterinsaari in the summer of 1934 and 1935. Ornis Fennica **13:** 137-139.

Turbott, E. G. 1940. A bird census on Taranga (the Hen). Emu **40:** 158-161.

Urner, C. A. 1930. Birds of Union County, N. J., and its immediate vicinity—a statistical study. Abst. Proc. Linn. Soc. N. Y. **39-40:** 44-98.

Van Deventer, William C. 1936. A winter bird community in western New York. Ecology **17:** 491-499.

Vevers, H. G., & James Fisher. 1936. A census of gannets on Ailsa Craig, with a new method of estimating breeding cliff populations. Journ. Animal Ecol. **5:** 246-251.

1938. The 1938 census of gannets (Sula bassana) on Ailsa Craig. Journ. Animal Ecol. **7:** 303-304.

Vevers, H. G., James Fisher, C. H. Hartley, & Alan T. Best. 1937. The 1937 census of gannets on Ailsa Craig; with notes on their diurnal activity. Journ. Animal Ecol. **6:** 362-365.

Vevers, H. G., & F. C. Evans. 1938. A census of breeding gannets (Sula bassana) on Myggenaes Holm, Faeroes. Journ. Animal Ecol. **7:** 298-302.

Vogt, William. 1942. An ecological depression on the Peruvian coast. Proc. 8th Amer. Sci. Cong. **3:** 507-527.

Waters, Martha. 1916. A census of forty acres in Indiana. Bird-Lore **18:** 373.

Watson, John B. 1907. Report of John B. Watson on the condition of the noddy and sooty tern colony on Bird Key, Tortugas, Florida. Bird-Lore **9:** 307-316.

Weaver, John E., & Frederic E. Clements. 1929. Plant Ecology. New York i-xx, 1-520.

Whitaker, J. R. 1916. A record bird census. Bird-Lore **18:** 248-249.

White, Katherine A. 1942. Frequency of occurrence of summer birds at the University of Michigan Biological Station. Wils. Bull. **54:** 204-210.

Wight, H. M. 1931. Quantitative methods in upland game bird investigation. Auk **48:** 553-558.

1934. The cover map and game census in pheasant management. Trans. 20th Amer. Game Conf. 329-333.

1939. Field and laboratory technic in wildlife management. Univ. Michigan Press, Ann Arbor 1-107.

Wild, S. V. 1935. A local bird census. Northwestern Nat. 111-117.

Williams, Arthur B. 1936. The composition and dynamics of a beech-maple climax community. Ecol. Mono. **6:** 317-408.

Williams, Cecil S., & William H. Marshall. 1937. Goose nesting studies on Bear River Migratory Waterfowl Refuge. Journ. Wildlife Manag. **1:** 77-86.

Williams, John. 1918. A vulture census and some notes. Wils. Bull. **25:** 75-83.

Wing, Leonard William. 1937. Further studies of wildlife cycles. Trans. 2nd Amer. Wildlife Conf. 326-339.

Wing, Leonard, & Millard Jenks. 1939. Christmas censuses—the amateur contribution to science. Bird-Lore **41:** 343-350.

Winkler, Wilhelm. 1930. Statistik der freilebenden Vögel. Verhandl. Zool.-Bot. Ges. Wein **80:** 53-58.

Winterbottom, J. M. 1936. Bird population studies; an analysis of the avifauna of the Jeanes School Station, Mazabuka, Northern Rhodesia. Journ. Animal Ecol. **5:** 294-311.

1938. On three bird censuses in woodland in Northern Rhodesia. Journ. Animal Ecol. **7:** 266-271.

1940. Bird population studies. The avifauna of Fort Jameson, Northern Rhodesia, 1935-38. Journ. Animal Ecol. **9:** 68-75.

1942. On the bird fauna of Kambule, Mongu, Northern Rhodesia. Journ. Animal Ecol. **11:** 205-214.

Wright, Howard W. 1913. The birds of San Martin Island, Lower California. Condor **15:** 207-210.

Wynne-Edwards, V. C. 1935. On the habits and distribution of birds on the North Atlantic. Proc. Boston Soc. Nat. Hist. **40:** 233-346.

Wynne-Edwards, V. C., & T. H. Harrisson. 1932. A bird census on Lundy Island (1930). Journ. Ecol. **20:** 371-379.

Wynne-Edwards, V. C., R. M. Lockley, & H. M. Salmon. 1936. The distribution and numbers of breeding gannets (Sula bassana L.). Brit. Birds **29:** 262-276.

Yapp, W. B. 1934. The rook population of West Gloucestershire. Journ. Animal Ecol. **3:** 77-80.

Zimmermann, Rud. 1932. Ueber quantitative Bestandsaufnahmen in der Vogelwelt. Mitheil. des Vereins sächs. Ornithol. **3:** 253-267.

APPENDIX 1. SCIENTIFIC NAMES OF BIRDS MENTIONED IN THE TEXT

Great-crested grebe, *Podiceps cristatus*
Fulmar, *Fulmarus glacialis*
Gannet, *Moris bassana*
Double-crested cormorant, *Phalacrocorax auritus*
Great blue heron, *Ardea herodias*
American egret, *Casmerodius albus*
White stork, *Ciconia ciconia*
Canada goose, *Branta canadensis*
Black brant, *Branta nigricans*
Black duck, *Anas rubripes*
Wood duck, *Aix sponsa*
Ring-necked duck, *Nyroca collaris*
Lesser scaup duck, *Nyroca affinis*
American merganser, *Mergus merganser*
Red-breasted merganser, *Mergus serrator*
Turkey vulture, *Cathartes aura*
Black vulture, *Coragyps atratus*
Cooper hawk, *Accipiter cooperi*
Red-tailed hawk, *Buteo borealis*
Red-shouldered hawk, *Buteo lineatus*
Rough-legged hawk, *Buteo lagopus*
Sparrow hawk, *Falco sparverius*
Ruffed grouse, *Bonasa umbellus*
Prairie chicken, *Tympanuchus cupido*
European partridge, *Perdix perdix*
Bob-white, *Colinus virginianus*
Valley quail, *Lophortyx californica*
Ring-necked pheasant, *Phasianus colchicus*
Lapwing, *Vanellus vanellus*
Woodcock, *Philohela minor*
Great Black-backed gull, *Larus marinus*
Herring gull, *Larus argentatus*
Ring-billed gull, *Larus delawarensis*
Black-headed gull, *Larus ridibundus*
Bonaparte gull, *Larus philadelphia*
Mourning dove, *Zenaidura macroura*
Yellow-billed cuckoo, *Coccyzus americanus*
Black-billed cuckoo, *Coccyzus erythropthalmus*
Screech owl, *Otus asio*
Great horned owl, *Bubo virginianus*
Barred owl, *Strix varia*
Short-eared owl, *Asio flammeus*
Saw-whet owl, *Cryptoglaux acadica*
Whip-poor-will, *Antrostomus vociferus*
Ruby-throated hummingbird, *Archilochus colubris*
Belted kingfisher, *Megaceryle alcyon*
Flicker, *Colaptes auratus*
Piliated woodpecker, *Ceophloeus pileatus*
Red-bellied woodpecker, *Centurus carolinus*
Red-headed woodpecker, *Melanerpes erythrocephalus*
Hairy woodpecker, *Dryobates villosus*
Downy woodpecker, *Dryobates pubescens*
Crested flycatcher, *Myiarchus crinitus*
Phoebe, *Sayornis phoebe*

Acadian flycatcher, *Empidonax virescens*
Alder flycatcher, *Empidonax traillii*
Least flycatcher, *Empidonax minimus*
Wood pewee, *Myiochanes virens*
Horned lark, *Otocoris alpestris*
Bank swallow, *Riparia riparia*
Rough-winged swallow, *Stelgidopteryx ruficollis*
Blue jay, *Cyanocitta cristata*
Crow, *Corvus brachyrhynchos*
Rook, *Corvus frugilegus*
Jackdaw, *Corvus monedula*
Black-capped chickadee, *Penthestes atricapillus*
Carolina chickadee, *Penthestes carolinensis*
Tufted titmouse, *Baeolophus bicolor*
White-breasted nuthatch, *Sitta carolinensis*
Red-breasted nuthatch, *Sitta canadensis*
Brown creeper, *Certhia familiaris*
European dipper, *Cinclus cinclus*
House wren, *Troglodytes aedon*
Carolina wren, *Thryothorus ludovicianus*
Catbird, *Dumetella carolinensis*
Brown thrasher, *Toxostoma rufum*
Robin, *Turdus migratorius*
Wood thrush, *Hylocichla mustelina*
Hermit thrush, *Hylocichla guttata*
Veery, *Hylocichla fuscescens*
Bluebird, *Sialia sialis*
Nightingale, *Luscinia megarhyncha*
Blue-gray gnatcatcher, *Polioptila caerulea*
Willow warbler, *Phylloscopus trochilus*
Chiff-chaff, *Phylloscopus collybita*
Golden-crowned kinglet, *Regulus satrapa*
Cedar waxwing, *Bombycilla cedrorum*
Starling, *Sturnus vulgaris*
White-eyed vireo, *Vireo griseus*
Yellow-throated vireo, *Vireo flavifrons*
Red-eyed vireo, *Vireo olivaceus*
Warbling vireo, *Vireo gilvus*
Black and white warbler, *Mniotilta varia*
Worm-eating warbler, *Helmitheros vermivorus*
Blue-winged warbler, *Vermivora pinus*
Yellow warbler, *Dendroica aestiva*
Magnolia warbler, *Dendroica magnolia*
Black-throated blue warbler, *Dendroica caerulescens*
Black-throated green warbler, *Dendroica virens*
Cerulean warbler, *Dendroica cerulea*
Blackburnian warbler, *Dendroica fusca*
Chestnut-sided warbler, *Dendroica pensylvanica*
Oven-bird, *Seiurus aurocapillus*
Louisiana water-thrush, *Seiurus motacilla*
Kentucky warbler, *Oporornis formosus*
Yellow-throat, *Geothlypis trichas*
Hooded warbler, *Wilsonia citrina*
Canada warbler, *Wilsonia canadensis*
Redstart, *Setophaga ruticilla*
English sparrow, *Passer domesticus*
Bobolink, *Dolichonyx oryzivorus*
Western meadowlark, *Sturnella neglecta*
Red-winged blackbird, *Agelaius phoeniceus*
Baltimore oriole, *Icterus galbula*
Cowbird, *Molothrus ater*
Scarlet tanager, *Piranga erythromelas*
Summer tanager, *Piranga rubra*
Cardinal, *Richmondena cardinalis*
Rose-breasted grosbeak, *Hedymeles ludovicianus*
Indigo bunting, *Passerina cyanea*
Purple finch, *Carpodacus purpureus*
Common redpoll, *Acanthis linaria*
Goldfinch, *Spinus tristis*
Towhee, *Pipilo erythrophthalmus*
Grasshopper sparrow, *Ammodramus savannarum*
Vesper sparrow, *Pooecetes gramineus*
Slate-colored junco, *Junco hyemalis*
Tree sparrow, *Spizella arborea*
Chipping sparrow, *Spizella passerina*
Field sparrow, *Spizella pusilla*
Fox sparrow, *Passerella iliaca*
Song sparrow, *Melospiza melodia*

IMPORTANT SPECIES OF THE MAJOR FORAGE TYPES IN COLORADO AND WYOMING

David F. Costello
Rocky Mountain Forest and Range Experiment Station[1]

[1] Maintained by Forest Service, U. S. Dept. of Agriculture, in cooperation with Colorado State College of Agriculture and Mechanic Arts at Fort Collins, Colorado.

TABLE OF CONTENTS

	PAGE
Introduction	109
Source and Nature of Data	109
Methods Used in Selecting Important Species	110
Grouping of data	110
Selection of Species	110
Important Species of the Great Plains	111
Short-grass type	111
Dry meadow type	113
Sand sagebrush type	113
Sagebrush type	114
Weed types	115
Important Species of the Mountain Region	116
Alpine and subalpine grassland type	116
Spruce-fir type	117
Lodgepole pine type	118
Aspen type	119
Ponderosa pine-Douglas fir type	121
Wet meadow type	122
Park type	123
Sagebrush type	125
Pinon-juniper type	126
Browse-shrub type	127
Important Species of the Semi-Desert Area	129
Sagebrush type	129
Saltbush type	130
Greasewood type	130
Discussion	131
Literature Cited	133

IMPORTANT SPECIES OF THE MAJOR FORAGE TYPES IN COLORADO AND WYOMING

INTRODUCTION

In order to organize studies and plan the use of range land effectively, it is common practice to base observations of the plant cover on only the most important species present. This selectivity is desirable and essential since critical analysis of the entire plant population is ordinarily impossible or, at least, impracticable.

The principle of selectivity of important species in reference to studies of range forage is illustrated by the work of many investigators. In preparing guides for determination of forage utilization in Montana, for example, Lommasson & Jensen (1938) used 16 important grasses. In a similar study on southwestern ranges, Crafts (1938) selected 11 species of grasses, chosen in order of their importance.

Most phenological investigations have also been limited to a relatively small number of species. Sampson & Malmsten (1926) in testing the effects of cropping vegetation at different stages of growth, limited their clipping to three grasses and two weeds and listed stages of development indicating range readiness for only the important forage species. Costello & Price (1939) in recording the results of a 10-year study of plant development in Utah confined their discussion principally to 13 important forage species. Craddock & Forsling (1938) in their study of spring-fall sheep range in Idaho listed prevalent forage species but presented detailed observations of the growth stages of only one grass, as being indicative of the influence of climate on grazing periods. Moreover, determinations of chemical composition of herbage and other technical studies have usually been restricted to selected plants of wide distribution and importance because of the amount of forage they produce (McCreary 1931, Gordon & Sampson 1939, Stoddart 1941).

In respect to the selection of important plants in planning actual range administration, numerous examples can be cited such as the use of indicator plants in judging range conditions and trends. Talbot (1937) lists both palatable plants and inferior but numerous plants as indicators of range conditions in the Southwest and cites specific examples of grasses and weeds which can be used as guides in recognizing range conditions. In a range handbook for California by the U. S. Forest Service (1939a) the important species to be used in judging range conditions are listed, while in a handbook by the U. S. Forest Service (1939) for the Intermountain region species are designated upon which management and utilization should be based.

Estimation of actual forage utilization is always based on selected species (Stoddart 1935, Pechanec & Pickford 1937; Canfield 1939); and, similarly, in making rough estimates of grazing capacity, only a few of the most important plants are considered.

Entirely aside from applied range management but closely related is the use of selected plants for ecological observations. In this field it is generally accepted that important plants, particularly the dominants, deserve concentrated study since they markedly reflect the impress of climate (Clements 1935) and react strongly to forces of the habitat (Sampson 1939).

Therefore, as this combined evidence indicates, it is essential or, at least, highly desirable in dealing with vegetation as forage to select the important species and concentrate observations and conclusions quite generally on these plants. As an aid in this selection for the plant types of a single region, this paper has been prepared.

The data presented are based on numerous recent forage inventories and range surveys in Colorado and Wyoming where more than 2,000 plant species were encountered and recorded. From these data and accompanying observations the following information for each major forage type has been compiled: (1) the most important plants; (2) the frequency of occurrence and relative amount of forage produced by these plants; and (3) a brief statement of the values of these plants in developing range management plans. This information is of immediate use to range administrators and should be of great value to ecologists and range research workers in planning future work in this area.

SOURCE AND NATURE OF DATA

Through the use of the square-foot density method of sampling vegetation (Stewart & Hutchings, 1936), data from 82,460 sample plots have been assembled by the Rocky Mountain Forest and Range Experiment Station from forage inventories, cooperative surveys,[2] and research projects. These data were obtained for every major range type in Colorado and Wyoming. More than 40,000 of the total number of plots were sampled by experiment station personnel. The accumulation of data from all sources has extended over the period, 1937 to 1942 inclusive. Many areas which were affected by the great drought of 1934 have been re-examined since 1940 in order to avoid presentation of a picture of the vegetation as affected by unusual weather conditions.

Species were listed by range types and their densities recorded on Form 764b of the Interagency Range Survey Committee Instructions (1937) or on

[2] Agencies participating in cooperative surveys were the Forest Service, Resettlement Administration, and Soil Conservation Service of the U. S. Department of Agriculture; the Division of Grazing of the U. S. Department of Interior; Colorado State College of Agriculture and Mechanic Arts; and the University of Wyoming.

similar forms. Plot data were supplemented by type descriptions and by notes on range conditions, forage utilization, season of use, class of livestock, and management practices. Notes were taken on the following items for important species: plant parts eaten; estimated percentage of each plant eaten; reaction to grazing; distribution in type; general vigor; reproduction; abundance in type; and special characteristics, including poisonous properties and spines or injurious devices.

METHODS USED IN SELECTING IMPORTANT SPECIES

GROUPING OF DATA[3]

The data were grouped by broad divisions of range land in Colorado and Wyoming, varying as to topography, climatic conditions, and grazing practices. The divisions recognized were the Great Plains, the semi-desert, and the mountain region (Fig. 1).

The data from individual plots and accompanying notes and comments were then grouped by range types within each of these broad categories. Not less than 1,000 sample plots were used in computing the species frequency of any type. The types were based on the standard classification (Interagency Range Survey Committee, 1937) excepting in those instances where subdivision appeared to be desirable. The following types and subtypes were encountered in the survey:

Type designation[4]	*Name of type*
Plains area	
1-S	Plains short-grass
2-D	Dry meadow
4	Sagebrush
4-S	Sand sagebrush
18	Weed
Mountain area	
1-A	Alpine and sub-alpine grassland
1-M	Mountain park
2-W	Wet meadow
4	Sagebrush
5	Browse-shrub
6-L	Lodgepole pine
6-P	Ponderosa pine-Douglas fir
6-S	Spruce-fir
9	Pinon-juniper
10	Aspen
Semi-desert area	
4	Sagebrush
13	Saltbush
14	Greasewood

Forage types are designated according to aspect or physiognomy. Admittedly the classification of vegetation into types on the basis of general appearance—grassland types, shrub types, and forest types—results in an artificial grouping for which an equivalent ecological terminology in many instances is not available. However, detailed investigation of the communities within each of these physiognomic units will be necessary before a natural or phylogenetic system of classification can be achieved that is acceptable to range technicians and ecologists alike.

The ecological rank of some of the types discussed in the following pages is reasonably clear, particularly those which are the equivalent of plant associations. The rank of others, when considered individually and locally, may be nothing more than societies or associes. Their proper place can be assigned only when their relation to the climax has been ascertained in terms of development.

The plains short-grass type, for example, is the equivalent of the mixed prairie of Clements & Shelford (1939), or more specifically the "omnipresent disclimax, the so-called short-grass plains" which it contains. The lack of agreement among ecologists on a designation for this community is indicated by the fact that more than 20 names have been assigned to it (Carpenter 1940, p. 645). The sand sagebrush type in eastern Colorado is the equivalent of the sand sage community of Ramaley (1939) and is nearly synonymous with the sand-hills mixed association of Shantz (1911). Considerable diversity in naming of plant communities is apparent when the classification of vegetation belts of the Rocky Mountain region by various workers including Merriam (1892), Ramaley (1927), Shreve (1915), Clements (1920), Tidestrom (1925) and others are compared. However, the recognition of types such as the spruce-fir association, the ponderosa pine-Douglas fir association, and the pinon-juniper association is made easy by their visibility. The aspen, lodgepole pine, and sagebrush types are developmental associations which are regarded by some workers as disclimaxes (Clements & Clements 1941). The weed types of the plains area are stages of the subsere which, without undue disturbance, will eventually blend into the climax.

The perennial forb type and the half shrub types were omitted because of their unstable nature and because of their great variation in species composition from one locality to another. The creosote bush, mesquite, winterfat, and desert shrub types, as characterized in the "Instructions for Range Surveys," do not occur or are of very limited extent in Colorado and Wyoming.

SELECTION OF SPECIES

Essentially, a score card system was used in evaluating the importance of each species in each range type. Frequency of occurrence was obtained by expressing in percentage the number of sample plots on which each species occurred. The percentage of usable forage furnished by each species in the type was obtained by dividing the species forage factor by the type forage factor (Interagency Range Survey Committee 1937), and multiplying by 100. The forage factor for a species is the product of its density and proper use factor or palatability.

All species within each type were then ranked in descending order according to their frequency and the amount of forage produced. Grasses and grass-

[3] Assistance of W.P.A. Projects 4294 and 5063 in compiling data is acknowledged.

[4] Type symbols follow in general the designations used in the "Instructions for Range Surveys."

like species, weeds (forbs), and browse[5] were segregated and ranked in order of descending importance within each group. Geographic distribution or occurrence in other range types was occasionally used as a criterion for shifting the order of importance of certain species listed in the tables in the text. Thus, in Table 1, galleta *(Hilaria jamesi)*[6] has a greater frequency and produces more forage for the short-grass type as a whole than does bluestem wheatgrass *(Agropyron smithi)*. The former, however, is much more limited in its distribution, being confined principally to southern Colorado, than is the latter. Consequently, the order of rating has been reversed. Other special characteristics, such as poisonous properties, have been used in making minor shifts in order of importance for various species. These shifts are not arbitrary but are based on judgment as influenced by voluminous notes and comments furnished by the field examiners.

In addition to the important species presented in the tables, a list of additional plants has been included in the text for each type. These species frequently are of importance only in local areas. Many of them are of low forage value or are limited in their distributions. Some are included only because of their numerical abundance in restricted localities.

IMPORTANT SPECIES OF THE GREAT PLAINS

The Great Plains area in Colorado extends eastward from the foothills of the Rocky Mountains. In Wyoming it extends eastward from a broad transition zone between sagebrush and short-grass which passes in a north-south direction through the east-central portion of the state (Fig. 1).

The plains area is gently rolling country with elevations from approximately 7,000 feet in some localities in the west to 3,500 feet in the east. Yearly precipitation varies from 7 to 18 inches. Much of the area is in range land on which yearlong grazing is practiced.

The short-grass type, characterized principally by blue grama *(Bouteloua gracilis)* and buffalograss *(Buchloe dactyloides)*, occupies the plains in the eastern parts of the two states. The big sagebrush *(Artemisia tridentata)* type dovetails with the short-grass type in east-central Wyoming or in many instances assumes the nature of a gradual transition, with the short-grasses prevailing as an understory beneath the sagebrush. Dry meadow types occur along the stream courses throughout the area. On the thousands of acres that have been plowed and then abandoned for dry farming the annual weed type is characteristic. This type represents a succession towards a short-grass cover.

In the tables which are presented the percentage of forage furnished by each species and the frequency of occurrence represent the average for the type. Specific localities will naturally show variation from the type as a whole. The occurrence of important species in other types is shown by type symbols[7] in the last column of each table.

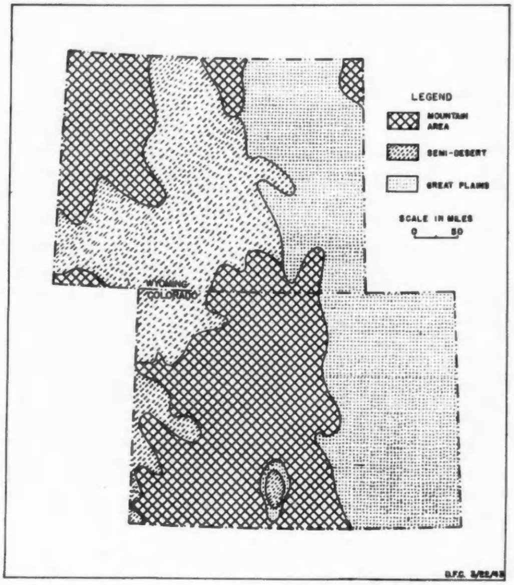

FIG. 1. Important species were listed by forage types within three broad divisions of range lands in Colorado and Wyoming.

SHORT-GRASS TYPE

Blue grama is the dominant species in the short-grass type and is the species on which range management should be based (Fig. 2). On well managed ranges it produces from 50 to 95 percent of all the forage furnished. In eastern Colorado, buffalograss commonly alternates with blue grama or is intermingled with it in varying proportions (Table 1),

FIG. 2. A good stand of blue grama in a lightly grazed pasture in eastern Colorado.

[5] Grasses, grasslike plants, weeds, and browse are the main groups into which western range plants are customarily divided. The term "weed" is here applied to herbaceous nongrasslike plants and is the equivalent of the ecological term "forb."

[6] Common names and the spelling of scientific names conform in general to the system used in "Standardized Plant Names," J. Horace McFarland Co. 1942.

[7] See page 110 for symbols.

while in eastern Wyoming it does not constitute an appreciable portion of the vegetal cover (Table 2). Clipping studies and extensive grazing intensity tests on the Central Plains Experimental Range[8] near Nunn, Colorado, indicate that maximum forage production on short-grass ranges is maintained when not more than 45 to 50 percent of the total seasonal weight production of these two grasses is utilized each year.

TABLE 1. Important species of the short-grass type (eastern Colorado).

Species	Frequency	Forage produced	Occurrence in other plains types
Grass and grass-like species:	*Percent*	*Percent*	
Bouteloua gracilis	94	71.0	All
Buchloe dactyloides	42	18.4	2-D
Aristida longiseta	25	0.8	18, 4-S
Agropyron smithi	13	0.4	4, 1-S (Wyo.), 18, 2-D
Hilaria jamesi	24	2.6	4-S
Stipa comata	11	0.2	4, 4-S, 1-S (Wyo.)
Carex filifolia	8	1.1	1-S (Wyo.), 4
Muhlenbergia torreyi	9	0.1	18
Weeds:			
Salsola kali tenuifolia	35	2.4	18, 4-S, 1-S (Wyo.)
Plantago purshi	25	0.0	1-S (Wyo.), 4, 4-S
Sphaeralcea coccinea	14	0.0	18, 1-S (Wyo.), 2-D, 4
Lepidium densiflorum	12	0.1	1-S (Wyo.)
Chenopodium album	10	0.0	All
Browse:			
Opuntia spp.[1]	38	0.0	1-S (Wyo.), 4, 4-S, 18
Artemisia frigida	19	0.1	1-S (Wyo.), 4
Gutierrezia sarothrae	11	0.0	2-D, 1-S (Wyo.), 4

[1]*Opuntia polyacantha, O. vulgaris*, and *O. rhodantha.*

TABLE 2. Important species of the short-grass type (eastern Wyoming).

Species	Frequency	Forage produced	Occurrence in other plains types
Grass and grass-like species:	*Percent*	*Percent*	
Bouteloua gracilis	82	65.0	All
Agropyron smithi	73	7.3	4, 1-S (Colo.), 18, 2-D
Poa arida	46	3.7	4
Stipa comata	41	3.9	4, 4-S, 1-S (Colo.)
Carex filifolia	23	6.0	4, 1-S (Colo.)
Koeleria cristata	18	0.7	4
Agropyron spicatum	10	1.8	4
Sporobolus cryptandrus	10	0.7	18, 2-D, 4-S
Festuca octoflora	11	0.2	......
Weeds:			
Chenopodium album	37	0.8	All
Plantago purshi	25	0.1	1-S (Colo.), 4, 4-S
Sphaeralcea coccinea	21	0.0	18, 1-S (Colo.), 2-D, 4
Lepidium densiflorum	19	0.0	1-S (Colo.)
Lappula redowski	15	0.0	18, 4
Salsola kali tenuifolia	10	0.3	18, 4-S, 1-S (Colo.)
Browse:			
Artemisia tridentata	54	3.0	4
Opuntia polyacantha	55	0.0	1-S (Colo.), 18, 4, 4-S
Artemisia frigida	22	0.3	1-S (Colo.), 4
Gutierrezia sarothrae	15	0.0	1-S (Colo.), 2-D, 4
Artemisia cana	13	0.5	4

On ranges which have been conservatively used for a number of years various taller grasses ("mid-grasses") such as red threeawn *(Aristida longiseta)*, bluestem wheatgrass *(Agropyron smithi)*, needleandthread *(Stipa comata)*, and sand dropseed *(Sporobolus cryptandrus)* tend to become abundant, although they seldom produce any outstanding volume of forage (Costello 1942). Under light grazing pressure, and in wet years, these grasses increase in abundance; under heavy grazing use, and in dry years they become inconspicuous and may practically disappear, leaving only the short-grasses if the drought or heavy use is long continued (Weaver & Albertson 1940, 1942). Prairie junegrass *(Koeleria cristata)*, bearded bluebunch wheatgrass *(Agropyron spicatum)*, and threadleaf sedge or "niggerwool" *(Carex filifolia)*, locally abundant in some areas, provide early spring forage before the short-grasses have produced much volume.

The weed species commonly associated with the short-grasses fluctuate greatly in density from year to year. The enormous stands of lambsquarters goosefoot *(Chenopodium album)*, prairie pepperweed *(Lepidium densiflorum)*, and western stickseed *(Lappula redowski)*, which occasionally develop in wet years are usually found on native short-grass sod which has suffered both from heavy grazing and drought. The indicator significance of these annual weed species and of sixweeks fescue *(Festuca octoflora)* which periodically dominate the landscape in the Great Plains is in need of further study.

The commonest browse species in the short-grass type are the pricklypears (*Opuntia* spp.). The investigations of Turner and Costello (1942) indicate that increase in abundance of these cacti, particularly plains pricklypear *(O. polyacantha)*, in recent years is related to a succession of drought seasons rather than excessive grazing. As a matter of fact, areas from which grazing animals are excluded sometimes support denser stands of pricklypear than moderately used ranges. (Cook 1942) also found indications that cacti increase in numbers during drought cycles and tend to decrease in wet periods. His conclusions were that a moth which tends to keep cactus in check finds more favorable conditions for its development during years of relatively high rainfall.

In eastern Wyoming, big sagebrush lends aspect to the short-grass type over many square miles, and under continuous heavy grazing invades the grassland and results in a change of forage type and a marked reduction in grazing capacity. Broom snakeweed *(Gutierrezia sarothrae)*, the presence of which is an indicator of overgrazing in some regions, is rather infrequent in occurrence and of doubtful value as a clue to overuse by livestock on eastern Colorado and Wyoming ranges. Decrease in grass density and increase in abundance of weeds are indicators that appear before snakeweeds become abundant and reflect the incipient rather than the later stages of overuse. When cattle are forced to eat broom snakeweed, however, the palatable grasses are liable to serious damage and as a rule the animals have already ceased their normal seasonal weight gain.

[8] A branch station maintained by the Rocky Mountain Forest and Range Experiment Station in cooperation with the Soil Conservation Service.

Additional species which may be important only in local areas or in certain years are included in the following list:

GRASS AND GRASSLIKE

Carex eleocharis
Munroa squarrosa
Sporobolus airoides

WEEDS

Astragalus spp.
Chrysopsis villosa
Cryptantha jamesi
Eriogonum effusum
Helianthus annuus
Phlox douglasi
Polygonum aviculare
Psoralea tenuiflora

BROWSE

Artemisia dracunculoides
Artemisia filifolia
Eurotia lanata
Gutierrezia longifolia

Dry Meadow Type

This type occurs in alkaline swales, on the borders of streams (Fig. 3) and frequently as one of the concentric vegetation zones bordering intermittent ponds that occur throughout the short-grass region in the eastern parts of Colorado and Wyoming. Although dry meadows in the Great Plains are usually not extensive, when properly maintained, they provide valuable winter range for cattle, thus complementing the short-grass type which furnishes the bulk of range forage during the summer grazing season.

FIG. 3. A dry meadow type characterized by inland saltgrass in an alkaline swale in eastern Colorado.

Inland saltgrass *(Distichlis stricta)* and alkali sacaton *(Sporobolus airoides)* are the dominant species and the plants upon which range management should be based (Table 3). Under moderate use these species contribute from 60 to 90 percent of the forage in a typical meadow and provide 4 to 6 times more winter grazing capacity than can be obtained from a similar area of the adjoining short-grass tpye. Bluestem wheatgrass is a secondary species which may be locally abundant where subsoil moisture is plentiful.

TABLE 3. Important species of the dry meadow type.

Species	Frequency	Forage produced	Occurrence in other plains types
Grass and grasslike species:	*Percent*	*Percent*	
Distichlis stricta	82	60.0	......
Sporobolus airoides	58	8.0	4-S, 1-S (Wyo.)
Buchloe dactyloides	49	4.6	......
Bouteloua gracilis	29	1.8	All
Agropyron smithi	22	0.2	4, 1-S, 18
Schedonnardus paniculatus	18	0.1	......
Weeds:			
Iva axillaris	38	0.0	......
Chenopodium album	33	0.2	All
Aster tanacetifolius	16	0.0	18
Sphaeralcea coccinea	10	0.0	18, 1-S (Wyo. & Colo.), 4
Browse:			
Chrysothamnus nauseosus	21	0.0	......
Atriplex canescens	18	0.6	......
Gutierrezia sarothrae	9	0.0	1-S (Colo. & Wyo.), 4

Consistent grazing of inland saltgrass to a height of 2 inches or less usually is accompanied by a reduction in volume of forage produced and invasion of the type by blue grama and buffalograss with consequent reduction in winter grazing capacity. Continued overuse of these areas may end in a subtype characterized by inferior grasses and weeds such as tumblegrass *(Schedonnardus paniculatus)*, poverty sumpweed *(Iva axillaris)*, lambsquarters goosefoot, tansyleaf aster *(Aster tanacetifolius)*, and scarlet globemallow *(Sphaeralcea coccinea)*.

Fourwing saltbush *(Atriplex canescens)* may be locally abundant. When present it indicates moderate alkalinity of the soil. Rubber rabbitbrush *(Chrysothamnus nauseosus)* and broom snakeweed, which occasionally become dominant, probably reflect moisture and edaphic factors more than they indicate degree of use by livestock.

Additional Species

GRASS AND GRASSLIKE

Carex eleocharis
Festuca octoflora
Hordeum jubatum
Juncus balticus
Sporobolus airoides
S. texanus

WEEDS

Chenopodium leptophyllum
Cleome serrulata
Grindelia squarrosa
Lepidium densiflorum
Monolepis nuttalliana

BROWSE

Eurotia lanata

Sand Sagebrush Type

This type is confined to sandy soils and its dominant species, sand sagebrush *(Artemisia filifolia)* al-

most invariably marks areas where the grazing capacity is moderate to low (50 to 90 acres per animal unit per year). It is the equivalent of the sand sage community as described by Ramaley (1939). Small soapweed *(Yucca glauca)* which occurs in this type is also an indicator of sand although it is not entirely confined to such soils.

Blue grama provides the bulk of the forage (Fig. 4) in the sand sagebrush type (Table 4) and management should be directed towards its perpetuation.

FIG. 4. Sand sagebrush type in southeastern Colorado, with an understory consisting principally of blue grama.

A mixture of taller grasses including needleandthread, red threeawn, and sand dropseed along with sand indicators such as prairie sandreed *(Calamovilfa longifolia)* and sand bluestem *(Andropogon halli)* usually occurs if grazing has been moderate for a number of years. Little bluestem *(Andropogon scoparius)* which dominated many of the sandhill areas in eastern Colorado 15 to 25 years ago now persists mostly on the borders of borrow pits along highways where moisture conditions are favorable and in cemeteries where the grazing influence has been eliminated. On areas which are heavily and continuously overgrazed, blue grama is commonly replaced by tumbling Russian thistle *(Salsola kali tenuifolia)*, lambsquarters goosefoot, woolly Indianwheat (*Plantago purshi*), *Eriogonum effusum* and other weeds. The pricklypears (*Opuntia vulgaris* and *O. polyacantha*) seldom become abundant and are of minor importance in this type.

TABLE 4. Important species of the sand sagebrush type.

Species	Frequency	Forage produced	Occurrence in other plains types
Grass and grass-like species:	*Percent*	*Percent*	
Bouteloua gracilis	78	57.2	All
Calamovilfa longifolia	54	1.6	......
Stipa comata	65	2.0	4, 1-S (Colo. & Wyo.)
Aristida longiseta	28	6.0	18, 1-S (Colo.)
Andropogon halli	38	0.6	......
Sporobolus cryptandrus	22	1.4	18, 2-D, 1-S (Wyo.)
Hilaria jamesi	12	5.0	1-S (Colo.)
Weeds:			
Salsola kali tenuifolia	50	4.4	18, 1-S (Colo. & Wyo.)
Chenopodium album	42	1.6	All
Ambrosia artemisifolia	36	0.0	......
Eriogonum effusum	18	0.9	......
Plantago purshi	11	0.2	1-S (Colo. & Wyo.), 4
Browse:			
Artemisia filifolia	94	8.4	......
Opuntia spp. [1]	18	0.0	1-S (Colo. & Wyo.), 18, 4
Yucca glauca	9	0.1	......

[1]*Opuntia polyacantha, O. vulgaris.*

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Andropogon scoparius
Carex eleocharis
Muhlenbergia pungens
Oryzopsis hymenoides
Redfieldia flexuosa

WEEDS

Abronia fragrans
Aplopappus spinulosus
Artemisia gnaphalodes
Chenopodium leptophyllum
Evolvulus pilosus
Gilia inconspicua
Helianthus petiolaris
Psoralea argophylla

BROWSE

Prunus besseyi

SAGEBRUSH TYPE

Big sagebrush gives a shrubby aspect to this type, although the major forage species is blue grama (Table 5). Taller grasses, particularly bluestem wheatgrass, needleandthread, plains bluegrass *(Poa arida)* and prairie junegrass, occur in this type, especially along the streams and valleys. These species become reestablished in wet cycles and tend to disappear in dry cycles (Larson, 1940). There is a tendency for these secondary grasses, together with threadleaf sedge and bearded bluebunch wheatgrass to be abundant on moderately used ranges but rare or absent on areas that have been subjected to continuous heavy grazing. In seasons with moderate to heavy rainfall these grasses tend to obscure the understory of blue grama (Fig. 5).

Weeds such as Douglas phlox *(Phlox douglasi)*, woolly Indianwheat, lambsquarters goosefoot, and western stickweed may occur in considerable density particularly on depleted ranges after heavy spring rainfall. On areas supporting a good grass cover these species and scarlet globemallow are common but seldom sufficiently abundant to obscure the blue grama sod even in seasons favorable to their growth.

Plains pricklypear is widely distributed throughout the sagebrush type and may be abundant on ranges in any condition. As in the short-grass type it is apparently an indicator of a series of drought years (Turner & Costello 1942). Fringed sagebrush *(Artemisia frigida)* and broom snakeweed occur most abundantly on ranges which are in poor condition as a result of past overutilization (Sarvis 1920). Silver sagebrush *(Artemisia cana)* is locally abundant and

FIG. 5. Big sagebrush type in east-central Wyoming, showing a fair stand of bearded bluebunch wheatgrass which obscures the understory of blue grama.

TABLE 5. Important species of the sagebrush type (east-central Wyoming).

Species	Fre-quency	Forage produced	Occurrence in other plains types
Grass and grass-like species:	*Percent*	*Percent*	
Bouteloua gracilis	68	41.5	All
Agropyron smithi	69	9.9	1-S (Colo. & Wyo.), 18, 2-D
Stipa comata	61	6.6	4, 4-S, 1-S (Colo. & Wyo.)
Poa arida	53	4.8	1-S (Wyo.)
Carex filifolia	44	10.5	1-S (Wyo. & Colo.)
Koeleria cristata	36	1.4	1-S (Wyo.)
Agropyron spicatum	28	5.3	1-S (Colo.)
Weeds:			
Phlox douglasi	33	0.0	......
Plantago purshi	29	0.1	1-S (Colo. & Wyo.), 4-S
Sphaeralcea coccinea	22	0.5	18, 1-S (Wyo. & Colo.), 2-D
Chenopodium album	20	0.5	All
Lappula redowski	20	0.0	18, 1-S (Wyo.)
Browse:			
Artemisia tridentata	73	9.0	1-S (Wyo.)
Opuntia polyacantha	45	0.0	1-S (Colo. & Wyo.), 18, 4-S
Artemisia frigida	34	0.5	1-S (Colo. & Wyo.)
Artemisia cana	28	3.2	1-S (Wyo.)
Gutierrezia sarothrae	21	0.0	1-S (Wyo. & Colo.), 2-D

occasionally alternates with big sagebrush, although the latter is better adapted to the drier sites than the former.

On areas where sheet and gully erosion have followed continuous overgrazing, big sagebrush may be practically the only plant in evidence. The few grasses that remain are generally found under the sagebrush plants and beyond the reach of grazing animals. Judgment of range recovery on such areas and management for restoration should nearly always be based on the grass stand and not on the degree to which big sagebrush is utilized.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Bromus tectorum
Distichlis stricta
Festuca octoflora
Oryzopsis hymenoides
Sitanion hystrix
Sporobolus cryptandrus

WEEDS

Cardaria draba
Chrysopsis villosa
Erigeron spp.
Grindelia squarrosa
Polygonum aviculare
Psoralea esculenta
Salsola kali tenuifolia

BROWSE

Artemisia pedatifida
Atriplex canescens
Atriplex gardneri
Cercocarpus montanus
Chrysothamnus lanceolatus
Eurotia lanata
Rhus trilobata
Yucca glauca

WEED TYPES

Throughout eastern Colorado and eastern Wyoming thousands of areas of varying size, formerly under cultivation, are now abandoned or are used for grazing. These areas are in all stages of plant succession from bare ground to practically complete stands of blue grama. The rate and nature of this secondary succession on abandoned fields has been described by Shantz (1911, 1917), Savage & Runyon (1937), Costello (1943), and others.

The early stages of natural recovery of vegetation on the Great Plains are characterized by annual and perennial weeds (Table 6). The species present on any specific area and their relative proportions are valuable clues to the length of time succession has been under way and to the proper grazing capacity.

On areas out of cultivation for one to five years, weeds commonly constitute the only vegetation with tumbling Russianthistle comprising 95 to 98 percent

TABLE 6. Important species of the weed types (abandoned fields).[1]

Species	Fre-quency	Forage produced	Occurrence in other plains types
Grass and grass-like species:	*Percent*	*Percent*	
Aristida longiseta	35	29.6	1-S (Colo.), 4-S
Sporobolus cryptandrus	24	21.0	4-S, 2-D, 1-S (Wyo.)
Agropyron smithi	21	11.8	4, 1-S (Colo. & Wyo.), 2-D
Munroa squarrosa	18	0.0	......
Muhlenbergia torreyi	12	0.6	1-S (Colo.)
Bouteloua gracilis	9	12.0	All
Weeds:			
Salsola kali tenuifolia	72	10.5	4-S, 1-S (Colo. & Wyo.)
Chenopodium album	64	5.0	All
Sphaeralcea coccinea	66	0.0	1-S (Wyo. & Colo.), 2-D, 4
Aster tanacetifolius	41	0.0	2-D
Lygodesmia juncea	30	0.0	......
Lappula redowski	30	0.0	1-S (Wyo.), 4
Cryptantha crassisepala	18	0.0	......
Grindelia squarrosa	12	0.0	......
Helianthus annuus	10	0.6	......
Gaura coccinea	10	0.1	......
Sophora sericea	9	0.0	18
Browse:			
Opuntia polyacantha	16	0.0	1-S (Colo. & Wyo.), 4, 4-S

[1]This table is a composite of the stages of vegetation recovery in the first 25 years after abandonment of cultivation. Space does not permit the inclusion of a table for each of the recognizable stages of succession that may be encountered even within a single township in the Great Plains.

of the total (Fig. 6). Occasionally the succession is initiated by a practically pure stand of common sunflower *(Helianthus annuus)*, prairie sunflower *(H. petiolaris)*, or lambsquarters goosefoot. Rather infrequently such grasses as sand dropseed and false buffalograss *(Munroa squarrosa)* may occur within the first five years. If cultivation has been practiced for only a few years (1 to 3) previous to abandonment, plains pricklypear and broom snakeweed may make an early appearance.

FIG. 6. Weed type in southeastern Colorado characterized by Russian thistles on wind drifted soil. The area has been out of cultivation for three years.

Areas abandoned for 6 to 10 years are generally characterized by a mixture of annual and perennial weeds such as tumbling Russianthistle (15 to 30 percent of the total composition), scarlet globemallow, rush skeleton-plant *(Lygodesmia juncea)*, curlycup gumweed *(Grindelia squarrosa)*, scarlet gaura (*Gaura coccinea)*, silky sophora *(Sophora sericea)*, and western stickseed. Sand dropseed, bluestem wheatgrass and an occasional clump of red threeawn may be present. In seasons of heavy rainfall this stage of vegetational development may result in death losses of cattle from bloating.

As the period of abandonment increases beyond 10 years the percentage of weeds rapidly decreases and grasses become increasingly abundant. Red threeawn is generally dominant after 15 to 20 years of succession (Fig. 7) and may not be entirely replaced by blue grama and buffalograss after 40 years.

Grazing capacity and forage utilization should be based on the grasses in in these recovery stages. Use should be conservative enough to insure maintenance and increase of the better forage plants. Tentative guides developed from study of these stages on the Central Plains Experimental Range in northeastern Colorado indicate that utilization of blue grama, red threeawn, sand dropseed, and bluestem wheatgrass should not exceed 20 percent of their volume until the weed population has been reduced in process of succession to one-fourth or less of the total vegetation cover.

FIG. 7. Red threeawn growing on road abandoned approximately 20 years. Blue grama is invading the edges of the road from the adjacent native range.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE
Hordeum jubatum
Schedonnardus paniculatus
Sitanion hystrix

WEEDS
Amaranthus blitoides
A. retroflexus
A. spinosus
Astragalus spp.
Cirsium undulatum
Dyssodia papposa
Iva axillaris
Oenothera pallida
Portulaca oleracea
Verbena bracteata
Xanthium spp.

BROWSE
Artemisia frigida
Gutierrezia sarothrae

IMPORTANT SPECIES OF THE MOUNTAIN REGION

The range types of the mountain region in Colorado and Wyoming occur principally at elevations greater than 5,000 feet. The alpine and subalpine grasslands occur above timberline where snow accumulations often exceed 10 feet in depth. The lower limit of this grassland type is generally bordered by the spruce-fir zone. Other major types encountered include spruce-fir, lodgepole pine, aspen, ponderosa pine-Douglas fir, wet meadows, parks which occur throughout a wide elevational range, and the sagebrush, pinon-juniper, and browse-shrub types which are most prominent at the lower elevations.

ALPINE AND SUBALPINE GRASSLAND TYPE

This type occurs in Colorado and Wyoming at elevations varying from 10,500 to more than 14,000 feet. Much of it is above timber line and consequently it is distinctive because of the absence of trees. Sedges, grasses, mosses, dwarf willows and

showy weed species constitute the characteristic vegetation. The growing season is short and these areas are grazed, principally by sheep, during the summer months.

Although sedges (*Carex* spp.) produce nearly 20 percent of the forage on the average within this type (Table 7) and occur more frequently than any other species, tufted hairgrass *(Deschampsia caespitosa)* is the most important single species. Management should be based on its perpetuation in areas where it forms a characteristic part of the flora. Thurber fescue *(Festuca thurberi)*, sheep fescue *(Festuca ovina)*, and purple pinegrass *(Calamagrostis purpurascens)* are rather sporadic in occurrence, although they may exhibit local abundance. Spike trisetum *(Trisetum spicatum)*, alpine bluegrass *(Poa alpina)*, and alpine timothy *(Phleum alpinum)* are generally present in the more mesophytic areas but owing to their scattered occurrence they seldom produce an appreciable amount of forage. Their gradual disappearance from the vegetal cover, however, may be an early indication of overuse by grazing animals. *Carex podocarpa* and *C. pseudoscirpoidea* are prominent in northwestern Wyoming.

TABLE 7. Important species of the alpine and subalpine grasslands.

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Carex spp.[1]	66	19.1	All
Deschampsia caespitosa	32	21.7	1-M, 2-W
Calamagrostis purpurascens	10	0.6	......
Festuca thurberi	7	4.8	10, 1-M
F. ovina	27	4.0	6-L, 6-S, 1-M
Trisetum spicatum	34	1.1	6-S, 6-L
Poa alpina	32	5.2	......
Phleum alpinum	17	2.5	2-W, 6-S
Weeds:			
Polygonum bistortoides	30	0.7	2-W
Potentialla spp.[2]	24	4.1	6-L, 1-M, 2-W, 4, 1-M
Caltha leptosepala	19	3.8	2-W
Chaenactis alpinum	10	0.0	......
Achillea lanulosa	8	0.3	All
Silene acaulis	20	2.7	......
Sieversia spp.[3]	16	1.2	......
Browse:			
Salix spp.[4]	11	2.9	......

[1]Includes *Carex atrata, C. bella, C. ebenea, C. festivella, C. nova, C. phaeocephala, C. podocarpa, C. pseudoscirpoidea*, and *C. substricta*.
[2]Includes *Potentilla glaucophylla*, and *P. pinnatisecta*.
[3]Includes *Sieversia ciliata*, and *S. turbinata*.
[4]Includes *Salix glauca acutifolia, S. petrophila*, and *S. saximontana*.

Weeds in considerable numbers, particularly the showy varieties, including American bistort *(Polygonum bistortoides)*, elkslip marshmarigold *(Caltha leptosepala)*, chaenactis *(Chaenactis alpinum)*, western yarrow *(Achillea lanulosa)*, and Parry townsendia *(Townsendia parryi)* are normal components of alpine grasslands which have been conservatively grazed (Fig. 8). *Kobresia bellardi* is common in southern Colorado but is not important northward. Under heavy grazing the usual decrease in grass

FIG. 8. Alpine grassland used by sheep for summer range. The vegetation consists of a good mixture of alpine bluegrass, spike trisetum, sedges, western yarrow and Parry townsendia. Big Horn National Forest.

cover and the disappearance of many of the showy weeds is accompanied by an increase in cinquefoils (*Potentilla* spp.), common dandelion *(Taraxacum officinale)*, and many low palatability weeds. On rocky soils and areas of low productive capacity dwarf tufted perennials such as moss silene *(Silene acaulis)*, which are characteristic of alpine summits throughout the Rocky Mountains may become especially abundant under continued heavy grazing. Proper use of alpine grasslands almost never results in a sward appearance with the broad leaved herbs grazed so closely as to be inconspicuous in the turf.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Juncus spp.

WEEDS

Erigeron spp.
Pseudocymopterus montanus
Sibbaldia procumbens
Thlaspi alpestre

BROWSE

Vaccinium scoparium

SPRUCE-FIR TYPE

This type, which is characterized principally by an overstory of Engelmann spruce *(Picea engelmanni)* and alpine fir *(Abies lasiocarpa)*, is best developed between elevations of 8,000 and 10,500 feet. The upper edge of this zone borders the alpine grasslands while the lower edge intermingles with a flora varying from grassy slopes to ponderosa pine *(Pinus ponderosa)* foothills. Grassland parks of various sizes commonly interrupt the spruce-fir type. Grasses and weeds characterize the understory to a greater extent than shrubs. This type is used extensively by both sheep and cattle for summer grazing.

The grazing capacity of most ranges in the spruce-fir type is comparatively low when contrasted with the alpine grasslands, the meadow type, and open stands of aspen or ponderosa pine. Individual grass

or weed species seldom become dominant and are generally scattered throughout the type. If the coniferous overstory is dense the ground may be almost bare of herbaceous vegetation and the forage species confined to the more open stands and small parks. Long continued overgrazing may result in almost pure stands of perennial weeds (Fig. 9) such as hairy goldaster *(Chrysopsis villosa)* and trailing fleabane *(Erigeron flagellaris)*.

FIG. 9. Open parks in the spruce-fir zone which have been heavily grazed by sheep for many years are frequently characterized by nearly pure stands of hairy goldaster.

Sedges as a group produce more forage than any other species in this type (Table 8), although like the grasses they are usually scattered irregu'arly over the range. Estimates of utilization should be

TABLE 8. Important species of the spruce-fir type.

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Carex spp.[1]	68	9.8	All
Trisetum spicatum	32	0.9	1-A, 6-L
Festuca ovina	18	1.3	6-L, 1-A, 1-M
Bromus anomalus	25	2.7	6-L, 10, 5
Phleum alpinum	15	1.8	2-W, 1-A
Stipa spp.[2]	7	3.1	4, 5
Elymus glaucus	6	0.9	10
Agrostis hiemalis	17	0.3	1-M
Poa reflexa	14	0.9	......
Weeds:			
Achillea lanulosa	53	3.6	All
Fragaria glauca	43	0.7	10, 1-M
Erigeron spp.[3]	26	0.9	2-W, 1-M, 4
Lathyrus leucanthus	12	1.4	10, 5
Senecio spp.[4]	23	0.8	......
Taraxacum officinale	19	4.8	All
Ligusticum porteri	6	1.1	......
Helenium hoopesi	10	0.0	1-M, 10
Browse:			
Vaccinium scoparium	17	0.0	6-L

[1]Principally *Carex festivella*, *C. geyeri*, *C. phaeocephala*, and *C. eleocharis*.
[2]Includes *Stipa columbiana* and *S. lettermani*.
[3]Principally *Erigeron asper*, *E. coulteri*, *E. salsuginosus*, *E. speciosus*, and *E. superbus*.
[4]Including *Senecio ambrosioides*, *S. serra*, *S. triangularis*, *S. rydbergi*, *S. bigelovi*, and *S. fendleri*.

made on the sedges, nodding brome *(Bromus anomalus)*, spike trisetum, and alpine timothy in preference to the low frequency grasses, such as nodding bluegrass *(Poa reflexa)*, winter bentgrass *(Agrostis hiemalis)*, blue wildrye *(Elymus glaucus)*, and subalpine needlegrass *(Stipa columbiana)*. Letterman needlegrass *(Stipa lettermani)* is common in the type in southwestern Colorado.

Weeds generally occur sporadically in the spruce-fir type. Occasionally small societies of fleabane (*Erigeron* spp.), groundsel (*Senecio* spp.) and western yarrow occur in moist areas where the crown canopy is open. Heavily grazed areas frequently support stands of blueleaf strawberry *(Fragaria glauca)*, common dandelion, Porter ligusticum *(Ligusticum porteri)* and orange sneezeweed *(Helenium hoopesi)*. This latter species is poisonous to sheep (Marsh, *et al*, 1921) and when present in quantity, management should be directed toward the minimum utilization of this species as well as conservative use of the grass and grasslike species (Cassady 1941, Doran 1942).

Grouse whortleberry *(Vaccinium scoparium)* is the only browse species which occurs in abundance in the spruce-fir type. On sandy or gravelly loams it frequently forms the understory of Engelmann spruce forests to the exclusion of practically all herbaceous species. It is browsed very little by cattle and sheep.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE
Koeleria cristata
Muhlenbergia montana
Poa pratensis

WEEDS
Agoseris spp.
Chrysopsis villosa
Geranium viscosissimum
Potentilla spp.
Pseudocymopterus montanus

BROWSE
Artemisia frigida
Vaccinium cespitosum

LODGEPOLE PINE TYPE

The lodgepole pine *(Pinus contorta latifolia)* type commonly alternates with the spruce-fir type at elevations of 8,000 to 11,000 feet. The two types are similar in that they are characterized by relatively large areas in which little palatable forage is available. Grasses commonly occur in isolated clumps or as scattered individuals. Red fescue *(Festuca rubra)* and sheep fescue provide the bulk of the forage (Table 9) and on recent burns may form fairly dense stands. Narrow leaved sedges are rather uniformly distributed throughout the type (Fig. 10) and, excepting the fescues (*Festuca* spp.), furnish more forage than all other grasses combined. Heavy use of the type is indicated when infrequent grasses such as nodding brome, timber danthonia *(Danthonia intermedia)*, and spike trisetum are sought by livestock and no ungrazed tufts remain.

TABLE 9. Important species of the lodgepole pine type.

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Carex spp.[1]	49	5.2	All
Festuca spp.[2]	17	12.3	6-S, 1-A, 1-M
Bromus anomalus	31	0.6	6-S, 10, 5
Danthonia intermedia	28	0.3	2-W
Trisetum spicatum	26	0.3	6-S, 1-A, 2-W
Weeds:			
Potentilla spp.	37	6.3	1-A, 1-M, 2-W, 4
Achillea lanulosa	32	1.4	All
Solidago spp.	26	1.3	......
Antennaria rosea	45	0.0	......
Lupinus wyethi	11	0.5	......
Galium boreale	9	0.0	10, 5
Browse:			
Vaccinium scoparium	24	0.0	6-S
Artemisia tridentata	23	4.1	4, 5, 9
Potentilla fruticosa	19	4.0	1-M, 2-W

[1]Principally *Carex heliophila*, and *C. geyeri*.
[2]Principally *Festuca rubra* and *F. ovina*.

FIG. 10. Elk sedge and wheatgrasses producing the bulk of the forage in an open lodgepole pine stand. Medicine Bow National Forest.

Weed species are seldom present in sufficient numbers to make a dense ground cover. Heavily used areas are commonly characterized by cinquefoils and western yarrow. Extensive areas are sometimes covered by rose pussytoes *(Antennaria rosea)* where the soil is otherwise barren of vegetation. Goldenrods (*Solidago* spp.), northern bedstraw *(Galium boreale)*, lupine *(Lupinus wyethi)* and other weeds are of such sporadic occurrence that they are of small value as indicators except in localized areas where the vegetational history of specific grazing allotments is known in detail.

Grouse whortleberry frequently forms pure stands in the understory as in the spruce-fir type. Bush cinquefoil *(Potentilla fruticosa)* commonly lends aspect to the moist open areas in the lodgepole pine type that are too small to be classified as meadows. Hedged appearance of these shrubs is an indication that the range as a whole is being overutilized. On drier sites in fairly open timber stands, big sagebrush is frequently a shrubby component of the understory. On the lower borders of lodgepole pine stands and as an alterne with aspen it sometimes indicates fairly recent fires (Clements, 1928, p. 299). Management of ranges where big sagebrush is prominent should be based on perpetuation of the grasses and weedy species.

If the vegetation of the larger parks in the lodgepole pine type is considered, Idaho fescue *(Festuca idahoensis)* is a prominent grass, particularly in northern Colorado. A common lodgepole pine understory in northern Colorado and in Wyoming is a pinegrass *(Calamagrostis rubescens)*-grouse whortleberry community.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Poa fendleriana
Stipa lettermani

WEEDS

Arnica cordifolia
Eriogonum subalpinum
Fragaria glauca
Lathyrus leucanthus

BROWSE

Arctostaphylos uva-ursi
Rosa woodsi

ASPEN TYPE

The aspen type occurs at elevations of 8,000 to 10,500 feet, depending largely on the exposure. In open stands of golden quaking aspen *(Populus tremuloides aurea)* that have been subjected to moderate grazing use the forage cover is generally excellent. It consists of a well balanced mixture of grasses, weeds, and shrubs, valuable for spring and summer grazing by both sheep and cattle (Fig. 11). Ten or fifteen species of grasses, 20 to 40 species of weeds, and several shrubs are not uncommonly recorded from a single area of 100 square feet. Individual species seldom become dominant in the aspen understory unless the effects of grazing or other disturbances are outstanding.

The larger parks, which are not included in the species lists for this type, frequently support excellent stands of Kentucky bluegrass *(Poa pratensis)*. This is the result, in many instances, of replacement of native bunchgrasses which have been used too heavily in the past. In the aspen type proper, mountain brome *(Bromus carinatus)* is one of the most important grasses (Table 10).

FIG. 11. Aspen type showing a good mixture of grasses, forbs, and shrubs. This area has been moderately grazed by sheep for several years.

TABLE 10. Important species of the aspen type.

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grasslike species:	*Percent*	*Percent*	
Carex spp.[1]	55	5.1	All
Bromus carinatus	25	11.7	......
Bromus anomalus	43	1.8	6-L, 6-S, 5
Elymus glaucus	20	1.5	6-S
Festuca thurberi	20	2.2	1-A, 1-M
Poa pratensis	26	10.6	5, 2-W, 6-P, 1-M
Festuca arizonica	13	1.3	6-P, 9, 4, 1-M
Koeleria cristata	14	0.6	4, 6-P, 1-M, 2-W, 9, 5
Weeds:			
Achillea lanulosa	72	2.9	All
Fragaria glauca	36	0.5	6-S, 1-M
Thalictrum fendleri	33	0.9	......
Taraxacum officinale	40	13.6	All
Vicia americana	30	1.1	4
Lathyrus leucanthus	29	3.7	6-S, 5
Galium boreale	29	0.1	6-L, 5
Helenium hoopesi	9	0.0	1-M, 6-S
Browse:			
Populus tremuloides aurea	61	0.1	......
Symphoricarpos oreophilus	29	3.9	5, 9, 6-P, 4
Rosa woodsi	14	0.9	6-P

[1]Principally *Carex festivella*, *C. geyeri*, *C. heliophila*, *C. eleocharis*, and *C. rostrata*.

Sedges as a group constitute the most important plants among the grass and grasslike species in the aspen type. For example, detailed observations in western Colorado disclosed that mature ewes in two bands of sheep spent from 10 to 17 percent of their grazing time eating sedges in the aspen and spruce-fir types (Cassady 1941a). More grazing time was spent on only one other species, mountain snowberry *(Symphoricarpos oreophilus)*.

Thurber fescue occasionally becomes abundant in open aspen stands as a result of long continued use by sheep. On driveways all weeds may disappear, leaving this species dominant in the understory. Nodding brome, Arizona fescue *(Festuca arizonica)*, prairie junegrass, and blue wildrye are generally scattered rather than grouped in more or less pure stands.

Western yarrow is the most frequent species in the aspen type and is a useful weed for making comparisons of range use and range conditions within the type. Its relative vigor, the number of flower stalks remaining ungrazed, and the abundance of plants are useful criteria in checking on livestock distribution and intensity of forage utilization. Blueleaf strawberry is common on areas where cattle concentrate. On moderately used ranges, Fendler meadowrue *(Thalictrum fendleri)*, American vetch *(Vicia americana)*, aspen peavine *(Lathyrus leucanthus)*, and northern bedstraw are almost constant components of the vegetation. Their absence generally may be construed as an indication of improper grazing management.

In western and southwestern Colorado, orange sneezeweed presents special problems of management in the aspen type (Cassady 1941). The manner in which these plants are grazed is an indication of the degree of use and a clue to the amount of death loss due to poison that may be expected. The heads of sneezeweed plants are usually grazed first, then the flower stem leaves, and finally the rosette leaves. When grazing results in utilization of flower heads, stem leaves and the tips of the rosette leaves, losses are liable to occur. Other outstanding weeds in southern Colorado sheep ranges are mountain thermopsis *(Thermopsis montana)* and porter ligusticum.

Mountain snowberry is the most important browse species in the aspen type. It is grazed closely by sheep wherever it is found and hence is a good indicator of utilization. Golden quaking aspen occurred on about 60 percent of the sample plots examined and in most instances represented aspen reproduction rather than the leaves and shoots of mature trees within the reach of livestock. The extent of damage to aspen by grazing animals may be used in recognizing the effect of grazing. Sampson (1919) states that in Utah over 90 percent of the damage inflicted on aspen reproduction results from browsing. Sheep are more destructive than cattle. "Observations covering a 5-year period in standing timber on sheep range showed that 27.2 percent of the reproduction was either injured or killed on lightly grazed plots, 31.8 percent on moderately grazed areas, and 65 percent on heavily grazed plots."

In wildlife management, aspen reproduction is very commonly used as an indicator of degree of use by deer and elk. Under heavy pressure from these game animals, even mature trees are sometimes "barked" and killed. It has been observed that one of the first results of overpopulation by deer and elk may be the complete elimination of aspen on localized winter concentration areas. Aspen trees are also extensively gnawed, ridden down, and otherwise destroyed in summer by elk. Packard (1942), in an investigation of aspens growing in Rocky Mountain National Park, Colorado, found that die-back is caused by a fungus *(Cytospora chrysosperma)*

which is introduced into healthy trees through wounds in the bark produced by various animals, including elk. He also found that reproductive growth is retarded by mule deer browsing the young shoots. The growth requirements, reproduction, and susceptibility to injury of aspen have been discussed in detail by Baker (1925) for the central Rocky Mountain region.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Agropyron pauciflorum
Bromus ciliatus
Festuca idahoensis
Stipa lettermani

WEEDS

Chrysopsis villosa
Delphinium barbeyi
Geranium spp.
Heracleum lanatum
Ligusticum porteri
Potentilla spp.
Pseudocymopterus montanus
Rudbeckia hirta
Senecio serra

BROWSE

Amelanchier alnifolia
Mahonia repens
Potentilla fruticosa
Prunus virginiana melanocarpa
Rosa spp.
Sambucus spp.

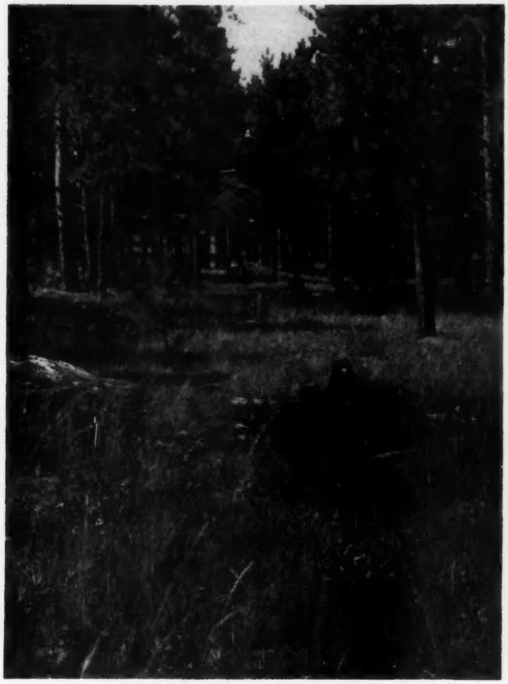

FIG. 12. A ponderosa pine stand with a good cover of perennial grasses, including Arizona fescue and mountain muhly.

PONDEROSA PINE-DOUGLAS FIR TYPE

The ponderosa pine-Douglas fir type is best developed between 5,000 and 8,000 feet elevation. It is characteristic of the foothills and lower mountain slopes. Ponderosa pine grasslands are used both for summer and winter range, particularly by cattle.

The better grazing areas in this type are characterized by open timber stands with a conspicuous ground cover of grasses and other herbaceous plants (Fig. 12). Areas dominated by a shrubby understory are exceptional. Various phases of this type may be distinguished on the basis of the predominant grass cover. In southeastern and southern Colorado blue grama is the principal grass, and with its associated species appears to constitute an extension of the short-grass type beneath the ponderosa pine overstory. Throughout the type in other parts of Colorado, Arizona fescue and other bunch forming grasses are typical of native ranges, while mountain muhly *(Muhlenbergia montana)* is locally dominant on the granitic soils in the Pikes Peak region. In Wyoming, wheatgrasses (*Agropyron* spp.), sedges, prairie junegrass, and species characteristic of the plains are common.

Sedges in the upper limits of this type merit special attention. The abundant narrow leaved species are threadleaf sedge, elk sedge *(Carex geyeri)*, sun sedge *(C. heliophila)*, and needleleaf sedge *(C. eleocharis)*. The amount of forage produced by sedges is indicated by the results of a clipping study made in central Colorado in late August 1938. Total average forage production was 262 pounds (air dry) per acre. In this instance, sedges comprised 58 pounds per acre or nearly one-fourth of the total weight of forage produced.

Kentucky bluegrass is an important component (Table 11) of the forage cover under certain conditions in the ponderosa pine-Douglas fir zone. Where moisture conditions are favorable, especially along stream bottoms, it frequently replaces the native bunchgrasses under even moderate grazing use. Under judicious management the sod may be maintained and an abundant supply of forage produced. Heavy use and trampling tends toward a replacement of the bluegrass by dandelions and other weeds.

Abandoned fields and severely overgrazed areas in this type are made conspicuous by heavy stands of fringed sagebrush, prairie sunflower and hairy goldaster. Spreading or mat forming species such as creeping mahonia *(Mahonia repens)* and rose pussytoes are generally found on thin soils, rocky areas, and sites where other vegetation is sparse. Woods rose *(Rosa woodsi)* is fairly common but rates low in palatability and when grazed to any extent by cattle or sheep indicates a shortage of the better forage species.

At the lower limits of the type, Douglas fir is no longer found and the ponderosa pines merge with the pinon-juniper type or give way to plains short-

TABLE 11. Important species of the ponderosa pine-Douglas fir type.

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Bouteloua gracilis	25	26.8	9, 4, 1-M, 5
Festuca arizonica	29	4.8	9, 4, 1-M, 5, 10
Carex spp.[1]	48	4.0	All
Koeleria cristata	35	2.1	4, 1-M, 2-W, 10, 9, 5
Poa pratensis	12	11.1	5, 1-M, 2-W, 10
Muhlenbergia montana	6	1.5	1-M
Weeds:			
Achillea lanulosa	43	1.3	All
Taraxacum officinale	21	3.2	All
Chrysopsis villosa	21	0.3	9, 5
Geranium spp.[2]	13	7.1	......
Orthocarpus luteus	10	0.0	4
Helianthus petiolaris	8	0.2	......
Browse:			
Artemisia frigida	43	0.8	9, 1-M, 5
Symphoricarpos oreophilus	20	4.2	5, 10, 9, 4
Mahonia repens	18	0.0	5
Rosa woodsi	12	0.7	10

[1]Principally *Carex filifolia*, *C. heliophila*, *C. eleocharis*, and *C. geyeri*.
[2]Includes *Geranium parryi*, *G. fremonti*, and *G. viscosissimum*.

grass or oak-brush. At elevations of 4,500 to 6,000 feet in southern Colorado from El Paso County south to Huerfano and Las Animas and west through Conejos, Archuleta, and La Plata counties in particular, the species composition is sufficiently different to justify a separate tabulation (Table 12).

TABLE 12. Important species of the ponderosa pine type (southern Colorado).

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Bouteloua gracilis	45	44.7	1-M, 5, 9, 4
Koeleria cristata	41	2.1	4, 1-M, 2-W, 10, 9, 5
Muhlenbergia montana	20	14.7	1-M
Festuca arizonica	16	8.9	1-M
Carex filifolia	13	0.8	5, 1-M
Poa pratensis	11	6.4	5, 1-M, 2-W, 10, 6-P
Weeds:			
Actinea richardsoni	23	0.0	1-M
Chrysopsis villosa	14	0.0	5, 9
Achillea lanulosa	13	0.1	5
Geranium parryi	12	0.1	......
Arenaria fendleri	8	0.0	......
Browse:			
Artemisia frigida	46	0.6	1-M, 5, 9
Cercocarpus montanus	13	2.8	5, 9

Blue grama is the principal forage species in this southern Colorado subtype and has apparently replaced the bunchgrasses, mountain muhly and Arizona fescue, in many localities. Under conservative use these latter two species maintain themselves in fairly dense stands but tend to disappear in favor of short-grass sod under heavy grazing pressure. On the drier sites threadleaf sedge is fairly common while on the moist valley bottoms and along streams, Kentucky bluegrass occasionally forms pure stands.

Throughout the ponderosa pine-Douglas fir type hairy goldaster occurs wherever the herbaceous density is low and grazing use is heavy. Fendler sandwort *(Arenaria fendleri)* and fringed sagebrush are likewise excellent indicators of overgrazing, although the latter is also a characteristic species in abandoned fields. Parry geranium *(Geranium parryi)* and western yarrow occur sporadically and when utilized to any considerable extent by livestock give evidence that the more important grass species are in danger of overuse.

True mountain mahogany *(Cercocarpus montanus)* is generally the most conspicuous browse species in this type. When it occurs in moderate abundance and is uniformly destributed it is an important indicator of utilization. In localities where it is sparse, the occasional plants may be heavily browsed and present a gnarled, stumpy, and dwarfed appearance without necessarily indicating overuse of the principal grasses. Livestock are prone to seek and over-utilize such occasional isolated species.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Agropyron smithi
Blepharoneuron tricholepis
Bromus anomalus
Danthonia intermedia
Festuca idahoensis
Poa secunda
Sitanion hystrix
Stipa comata

WEEDS

Actinea richardsoni
Erigeron spp.
Eriogonum umbellatum
Fragaria glauca
Geranium spp.
Helianthus petiolaris
Penstemon spp.
Potentilla spp.
Senecio spp.
Vicia americana

BROWSE

Arctostaphylos uva-ursi
Artemisia tridentata
Cercocarpus montanus
Mahonia repens
Opuntia sp.
Quercus spp.
Rosa woodsi

WET MEADOW TYPE

Wet meadows occur throughout the various mountain forage types at elevations of 5,000 to more than 10,000 feet in situations where the moisture content of the soil remains high throughout the growing season (Fig. 13). Sedges are dominant in these areas (Table 13). Excessive grazing tends to kill out the sedges and bring about their replacement by weeds such as dandelions and cinquefoils. Range utilization standards should be based on the degree of use that the sedges and more abundant grasses, such as tufted hairgrass, can withstand. Kentucky

FIG. 13. Wet meadow characterized by sedges, rushes, and moisture enduring grasses.

bluegrass occasionally forms a good sod in moist well drained meadows where it has replaced the native species and in such instances it is an indicator of moderately heavy grazing. Prairie junegrass and timber danthonia are generally confined to the drier margins of wet meadows and are seldom present in sufficient abundance to influence grazing capacity. Their gradual encroachment on the meadow, however, may be evidence that improper use is driving out the characteristic species.

TABLE 13. Important species of the wet meadow type.

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Carex spp.[1]	79	31.0	All
Deschampsia caespitosa	46	16.7	1-A, 1-M
Phleum alpinum	27	2.6	6-S, 1-A
Poa pratensis	5	0.8	5, 1-M, 10, 6-P, 2-W
Hordeum nodosum	9	0.3	......
Koeleria cristata	12	0.3	4, 6-P, 1-M, 10, 5
Danthonia intermedia	9	1.0	6-L
Weeds:			
Caltha leptosepala	28	2.5	1-A
Achillea lanulosa	33	1.8	All
Taraxacum officinale	24	9.8	All
Erigeron spp.[2]	26	0.8	6-S, 1-M, 4
Potentilla spp.[3]	28	0.5	6-L, 1-A, 1-M, 4
Polygonum bistortoides	19	0.3	1-A
Veronica alpina	8	0.0	......
Browse:			
Potentilla fruticosa	11	0.6	6-L, 1-M

[1]Includes *Carex aquatalis*, *C. atrata*, *C. ebenea*, *C. festivella*, *C. rostrata*, *C. substricta*, *C. heliophila*, *C. angustior*, *C. disperma*, and *C. egglestoni*.
[2]Includes *Erigeron acris*, *E. compositus*, *E. coulteri*, and *E. salsuginosus*.
[3]Includes *Potentilla anserina*, *P. filipes*, and *P. glaucophylla*.

Excessive numbers of western yarrow, dandelion, cinquefoils, and fleabane may denote heavy grazing use and may call for a change in class of livestock, a reduction in grazing intensity, or better distribution of animals. Elkslip marshmarigold, alpine speedwell *(Veronica alpina)*, and other moisture loving species generally present in wet meadows are indicators of a hydrophytic habitat and may possess little grazing significance.

Bush cinquefoil appears to be the most common shrub in wet meadows. It is an excellent yardstick for judging utilization. A heavily browsed or hedged appearance of this species is a manifestation of continued overuse of the meadow. Willows (*Salix* spp.) likewise give evidence of excessive use of meadows when they present a "browse line" or give evidence of having been denuded of their foliage.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE
Festuca ovina
Juncus balticus
Phleum pratense
Trisetum spicatum

WEEDS
Cicuta occidentalis
Epilobium adenocaulon
Gentiana thermalis
Ligusticum porteri
Pedicularis groenlandica
Senecio spp.
Trifolium repens
Veratrum californicum
Wyethia amplexicaulis

BROWSE
Salix spp.

PARK TYPE

Grasses are the predominant species in this type which occurs within wide altitudinal limits in the park-like openings in the browse or timbered zones (Fig. 14). Sedges, particularly of the narrow leaved variety, are abundant (Table 14), but generally not conspicuous. Characteristically, both grass and weed species are scattered in a more or less uniform mixture, although bunch forming fescues, tufted hairgrass, and Kentucky bluegrass may occur in relatively pure stands depending on habitat conditions and past grazing use.

A preponderance of weeds and a relative scarcity of grasses practicallly always follows improper man-

FIG. 14. Dry meadow in the aspen-spruce zone, characterized by a good stand of perennial grasses.

agement of this type. An abundance of low value species such as Douglas knotweed *(Polygonum douglasi)* generally indicates excessive deterioration of the forage cover and susceptibility to erosion. In park areas in the aspen and spruce-fir zones in western and southern Colorado orange sneezeweed is a common component of the dry meadow type and when it is abundant, sheep management practices must be designed to prevent losses from poisoning.

TABLE 14. Important species of the park type at higher altitudes.

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Carex spp.[1]	56	5.2	All
Poa pratensis	7	0.4	5, 2-W, 10, 6-P
Deschampsia caespitosa	13	4.3	2-W, 1-A
Koeleria cristata	24	0.4	4, 6-P, 2-W, 9, 5
Festuca ovina	15	1.2	6-L, 6-S, 1-A
Agrostis hiemalis	21	0.4	6-S
Festuca idahoensis	12	2.0	4
F. thurberi	12	1.1	10, 1-A
F. arizonica	11	1.1	6-P, 9, 4, 10
Weeds:			
Taraxacum officinale	55	22.4	All
Achillea lanulosa	67	3.6	All
Potentilla spp.[2]	53	2.7	6-L, 1-A, 2-W, 4
Erigeron spp.[3]	45	2.0	6-S, 2-W, 4, 9
Helenium hoopesi	20	0.0	6-S, 10
Fragaria glauca	19	1.8	6-S, 10
Polygonum douglasi	12	0.6	......
Browse:			
Artemisia frigida	18	1.7	9, 6-P, 5
Potentilla fruticosa	20	2.5	2-W, 6-L

[1]Includes *Carex aquatilis, C. festivella, C. geyeri, C. heliophila, C. phaeocephala, C. angustior, C. lanuginosa,* and *C. siccata.*
[2]Includes *Potentilla anserina, P. concinna, P. effusa, P. filipes,* and *P. glaucophylla.*
[3]Includes *Erigeron acris, E. ampla, E. asper, E. compositus, E. coulteri, E. corymbosus, E. eatoni, E. flagellaris, E. salsuginosus, E. speciosus,* and *E. uniflorus.*

Bush cinquefoil may be abundant in localized areas. Fringed sagebrush in abundance generally suggests overuse.

Both parks and wet meadows are key areas since they are congregation centers for livestock. If they are properly used, surrounding forage types usually will be maintained in good condition. Hence, a critical knowledge of the indicator values of important species in swales, creek bottoms, and grassy parks should be sought by range administrators.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Agropyron pauciflorum
Agrostis hiemalis
Blepharoneuron tricholepis
Bouteloua gracilis
Bromus anomalus
Muhlenbergia filiculmis
Stipa columbiana
Stipa lettermani

WEEDS

Actinea richardsoni
Antennaria rosea
Ligusticum porteri
Orthocarpus luteus
Penstemon spp.
Trifolium repens

BROWSE

Chrysothamnus spp.

Included in the park type, for purposes of this study are grasslands typical of the broad valley floors and gentle slopes between the major mountain ranges in central and southern Colorado. Their species composition differs from that of the mountain parks or grasslands at higher elevations.

Although blue grama is a nearly constant species and is the most important forage producer (Table 15) these areas do not properly belong in the short-grass type owing to an admixture of bunch forming species and taller varieties such as mountain muhly, Idaho fescue, bluestem wheatgrass, and prairie junegrass. In many ways these grasslands represent a mixture of elements from the plains with those from the higher and somewhat more mesophytic dry mountain meadows.

TABLE 15. Important species of the park type at lower altitudes.

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Bouteloua gracilis	84	65.1	5, 9, 4, 6-P
Muhlenbergia montana	52	22.0	6-P
M. torreyi	17	0.1	......
Koeleria cristata	20	0.3	4, 6-P, 2-W, 9, 5
Agropyron smithi	14	0.2	4, 5, 9
Festuca arizonica	13	0.9	6-P, 9, 4, 10
Carex filifolia	10	0.2	5, 6-P
Weeds:			
Actinea richardsoni	27	0.0	6-P
Salsola kali tenuifolia	20	0.6	9
Sphaeralcea coccinea	12	0.0	4, 9, 5
Browse:			
Artemisia frigida	55	0.5	6-P, 5, 9
Chrysothamnus spp.[1]	18	0.0	......
Eurotia lanata	15	0.7	......

[1]Includes *Chrysothamnus depressus, C. bigelovi,* and *C. lanceolatus.*

Abundant evidence indicates that blue grama has invaded many areas formerly dominated by bunchgrasses. In the light of present knowledge, management is best based on whichever grass is dominant at present in any specific locality.

As in the short-grass type an abundance of such species as ring muhly *(Muhlenbergia torreyi)*, tumbling Russian thistle, and fringed sagebrush is a mark of unsatisfactory range condition. Long continued overuse is followed in many instances by an invasion of various species of rabbitbrush (*Chrysothamnus* spp.). Pingue actinea *(Actinea richardsoni)* is frequent in these grasslands and deserves consideration because of its poisonous properties.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Aristida longiseta
Carex geyeri
Festuca idahoensis

Muhlenbergia filiculmis
Sitanion hystrix
Sporobolus cryptandrus

WEEDS

Arenaria fendleri
Potentilla spp.

BROWSE

Atriplex canescens
Gutierrezia sarothrae
Opuntia spp.

SAGEBRUSH TYPE

Big sagebrush gives the dominant aspect in this type (Fig. 15). Many mountainous areas where big sagebrush is now established, formely supported luxuriant stands of grasses and belonged in the park types, and in these areas herbaceous plants in the sagebrush type at the higher elevations (Table 16) are secondary in ecological importance but they are still the primary forage species. Where stands of sagebrush are well developed, use of this shrub must be considered under good grazing practices, but maintenance of the grass cover is the first requisite. Sagebrush seedlings invading grassy areas should be taken as indication that a change in grazing practices is essential. All sagebrush types, however, should not be construed as evidence of overgrazing in the past.

FIG. 15. Sagebrush type at 9,500 feet. The principal herbaceous species are prairie junegrass, Arizona fescue, Letterman needlegrass, western yarrow, and American vetch.

Sagebrush types in good condition are characterized by ample growth of the principal grasses between the sagebrush clumps. Unsatisfactory condition is evidenced when the important grasses survive only under the individual sagebrush clumps and undesirable or inferior weed species become prevalent between the clumps.

The weed species which increase in abundance under heavy use are common dandelion, western yarrow, yellow owlclover *(Orthocarpus luteus)*, Douglas knotweed, and various species of fleabane and cinquefoil. With increasing deterioration, pussytoes (*Antennaria* spp.), sandworts (*Arenaria* spp.), orange sneezeweed, and asters (*Aster* spp.) may become temporarily abundant to be followed by almost complete disappearance of the ground cover and the initial stages of sheet and gully erosion.

TABLE 16. Important species of the sagebrush type at higher altitudes.

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Koeleria cristata	43	3.0	6-P, 1-M, 2-W, 4, 9, 5
Carex spp.[1]	30	3.6	All
Stipa columbiana	33	9.0	6-S, 5
S. lettermani	21	1.1	5, 6-S
Agropyron smithi	18	1.3	5, 9, 1-M
Sitanion hystrix	19	0.2	9
Festuca arizonica	19	1.1	6-P, 9, 1-M, 4
Weeds:			
Taraxacum officinale	29	13.4	All
Achillea lanulosa	44	2.9	All
Orthocarpus luteus	15	4.2	6-P
Erigeron spp.[2]	24	2.2	6-S, 2-W, 1-M, 9
Vicia americana	18	0.3	10
Polygonum douglasi	18	0.1	5, 2-D
Potentilla spp.[3]	14	0.7	6-L, 1-A, 1-M, 2-W
Browse:			
Artemisia tridentata	80	23.2	6-L, 5, 9
Chrysothamnus lanceolatus	19	0.0	......
Symphoricarpos oreophilus	9	0.6	5, 10, 9, 6-P
Purshia tridentata	11	1.6	......

[1]Principally *Carex festivella*, *C. heliophila*, *C. rostrata*, *C. eleocharis*, *C. phaeocephala*, and *C. filifolia*.
[2]Principally *Erigeron speciosus*, *E. flagellaris*, *E. eatoni* and *E. corymbosus*.
[3]Principally *Potentilla argentea*, *P. filipes*, and *P. glaucophylla*.

In the big sagebrush areas on mountain slopes in western and southwestern Colorado, mountain snowberry, lanceleaf rabbit brush *(Chrysothamnus lanceolatus)* and antelope bitterbrush *(Purshia tridentata)* are important components of the shrubby cover. On sheep ranges the preservation of the latter two species may assume equal importance with the perpetuation of the more important grasses.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Festuca idahoensis
Festuca thurberi
Hordeum nodosum
Phleum pratense
Poa fendleriana
Poa pratensis
Poa secunda

WEEDS

Arenaria congesta
Aster spp.
Chrysopsis villosa
Delphinium geyeri
Helenium hoopesi
Orthocarpus luteus

BROWSE

Artemisia cana
Chrysothamnus viscidiflorus pumilus

On the lower mountain slopes, foothills, and mountain valleys the big sagebrush type is common, and the species composition is sufficiently different from

that of sagebrush areas in the higher elevations to merit a separate listing and discussion of species.

Blue grama is the outstanding forage producing grass (Table 17) in this type throughout south-central Colorado, and particularly in the San Luis Valley. Utilization standards should be based on this species when it is abundant rather than on big sagebrush. Blue grama is likewise the key to use in comparisons of grazing capacity between different areas wtihin the type. Scattered plants of bluestem wheatgrass, prairie junegrass, Scribner needlegrass *(Stipa scribneri)* and Indian ricegrass *(Oryzopsis hymenoides)* occur throughout. When these species are increasing from year to year range improvement is indicated.

TABLE 17. Important species of the sagebrush type at lower altitudes.

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Bouteloua gracilis	30	30.2	1-M, 5, 9, 6-P
Agropyron smithi	48	6.1	5, 1-M, 9
Koeleria cristata	25	1.3	5, 6-P, 1-M, 10, 2-W, 9
Sitanion hystrix	22	0.5	9
Stipa scribneri	18	3.1	......
Festuca idahoensis	8	2.2	1-M
Oryzopsis hymenoides	6	0.2	9
Weeds:			
Sphaeralcea coccinea	11	0.4	9, 1-M, 5
Phlox bryoides	10	0.0	......
Browse:			
Artemisia tridentata	94	33.2	9, 5, 6-L
Chrysothamnus viscidiflorus tortifolius	14	0.6	......
Gutierrezia sarothrae	20	0.0	9
Chrysothamnus lanceolatus	10	0.5	5

Weeds are seldom abundant in this type. Scarlet globemallow is a characteristic weed under a variety of forage conditions. Squarestem phlox *(Phlox bryoides)* becomes increasingly evident on denuded areas and on sites made susceptible to erosion by excessive grazing and trampling.

Broom snakeweed, twistleaf Douglas rabbitbrush *(Chrysothamnus viscidiflorus tortifolius)*, and lanceleaf rabbitbrush occur most frequently on ranges in unsatisfactory condition and are indicative of lower than average grazing capacity.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Agropyron spicatum
Muhlenbergia montana
Poa secunda
Sporobolus airoides
Stipa comata
Stipa lettermani

WEEDS

Actinea richardsoni
Astragalus spp.
Eriogonum spp.
Phlox spp.
Salsola kali tenuifolia

BROWSE

Artemisia cana
Artemisia nova
Atriplex canescens
Cercocarpus montanus
Chrysothamnus spp.
Purshia tridentata
Quercus utahensis
Symphoricarpos oreophilus

PINON-JUNIPER TYPE

The aspect of this type is determined by pinon and juniper (Fig. 16) and is distinctive wherever it occurs. The grazing understory, however, includes many combinations of grass, weed, and browse species. The outstanding forage species of the type is blue grama (Table 18) and where this grass dominates the grazing understory, management may be based on it alone. In localized areas Arizona fescue occasionally dominates the herbaceous cover. Needle-andthread, galleta, sand dropseed, and bluestem wheatgrass are sporadic in occurrence and generally grow in scattered clumps.

FIG. 16. Pinon type in southwestern Colorado showing sparse forage cover of bluestem wheatgrass and rabbitbrush. This area has been heavily grazed by sheep for many years.

Indian ricegrass is more characteristic of rocky areas and barren slopes where the topography is uneven and soil conditions are not always favorable. It is a good indicator of conservative grazing when it is present in such situations and has been moderately utilized. Bluestem wheatgrass is confined largely to

the moist areas in this type and is seldom an important component of the forage cover. Bottlebrush squirreltail *(Sitanion hystrix)* is distinctly an inferior species and appears principally on denuded areas.

TABLE 18. Important species of the pinon-juniper type.

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Bouteloua gracilis	45	56.9	1-M, 5, 4, 6-P
Festuca arizonica	31	4.5	6-P, 4, 1-M, 10
Hilaria jamesi	14	6.3	......
Koeleria cristata	12	1.3	4, 6-P, 9, 4, 1-M, 5, 10
Oryzopsis hymenoides	18	0.8	4
Sitanion hystrix	10	0.1	4
Agropyron smithi	10	1.5	4, 5, 1-M
Weeds:			
Erigeron spp.	33	0.2	6-S, 2-W, 1-M, 4
Chrysopsis villosa	15	0.1	6-P, 9, 5
Salsola kali tenuifolia	12	0.9	1-M
Sphaeralcea coccinea	9	0.0	4, 1-M, 5
Browse:			
Artemisia tridentata	34	14.0	4, 5, 6-L
Symphoricarpos oreophilus	23	4.3	5, 10, 6-P, 4
Pinus cembroides edulis	36	0.0	......
Juniperus spp.[1]	22	0.0	......
Gutierrezia sarothrae	15	0.0	4
Artemisia nova	14	0.0	......
Cercocarpus montanus	7	4.1	6-P, 5
Artemisia frigida	14	0.1	1-M, 6-P, 5
Yucca glauca	19	0.0	......

[1]Includes *Juniperus utahensis* and *J. monosperma.*

Weeds seldom become abundant in this type, even under good management. The common species such as hairy goldaster, tumbling Russian thistle, scarlet globemallow, lambsquarters goosefoot, and curlycup gumweed have little value as forage and are mainly indicators of the dry site conditions under which they grow.

True mountain mahogany, big sagebrush and mountain snowberry are the chief browse species. Antelope bitterbrush *(Purshia tridentata)* is abundant in some localities but is not characteristic of the type over extensive areas. The extent of cropping of the palatable browse species by grazing animals is one of the most valuable clues to the degrees of use and the range condition of specific areas. The cropping of juniper is a good measure of deer concentration in this type during the winter, particularly in western Colorado. Fringed sagebrush and broom snakeweed in fair abundance are early signs of range deterioration in the pinon-juniper type.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Aristida fendleriana
Aristida longiseta
Bouteloua curtipendula
Buchloe dactyloides
Carex filifolia
Sporobolus cryptandrus
Stipa lettermani
Stipa robusta

WEEDS

Actinea richardsoni
Aplopappus sp.
Astragalus spp.
Chrysopsis villosa
Erigeron spp.
Helianthus petiolaris
Pentstemon spp.
Sphaeralcea dissecta
Viguiera multiflora

BROWSE

Amelanchier alnifolia
Artemisia frigida
Atriplex canescens
Cercocarpus ledifolius
Cercocarpus montanus
Chrysothamnus spp.
Eurotia lanata
Holodiscus dumosus
Gutierrezia sarothrae
Opuntia sp.
Prunus virginiana melanocarpa
Purshia tridentata
Quercus spp.
Rhus trilobata
Ribes inerme

BROWSE-SHRUB TYPE

Although the general aspect or physiognomy of this type is essentially the same wherever it occurs, the floristic composition varies sufficiently to justify a division into eastern and western conditions (Tables 19 and 20). On the east front of the Rocky Mountains this type is dominant in the transition zone between the short-grass plains and the timbered areas of the foothills. In western and southwestern Colorado it occurs on the lower mountain slopes at the upper border of the sagebrush and pinion juniper zones.

TABLE 19. Important species of the browse-shrub type (eastern Colorado).

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	*Percent*	*Percent*	
Bouteloua gracilis	69	51.8	1-M, 9, 4, 6-P
Agropyron smithi	42	1.7	4, 1-M, 9
Carex filifolia	36	4.5	6-P, 1-M
Stipa comata	34	1.9	......
Koeleria cristata	34	1.1	6, 6-P, 9, 4, 1-M, 10
Stipa lettermani	21	1.2	4, 5, 6-S
Bromus tectorum	11	0.2	......
Weeds:			
Achillea lanulosa	65	1.9	All
Chrysopsis villosa	20	0.0	6-P
Helianthus annuus	14	0.1	......
Sphaeralcea coccinea	12	0.0	4, 9, 1-M
Taraxacum officinale	34	4.0	All
Browse:			
Artemisia frigida	48	1.8	1-M, 6-P, 9
Cercocarpus montanus	30	12.1	6-P, 9
Quercus gambeli	33	7.2	......
Rhus trilobata	15	0.0	......
Chrysothamnus lanceolatus	12	0.6	4

TABLE 20. Important species of the browse-shrub type (western Colorado).

Species	Frequency	Forage produced	Occurrence in other mountain types
Grass and grass-like species:	Percent	Percent	
Carex spp.	49	3.1	All
Koeleria cristata	32	2.1	4, 6-P, 9, 4, 1-M, 10
Stipa lettermani	32	2.0	6-S, 4
Agropyron smithi	34	1.6	4, 1-M, 9
Poa pratensis	20	8.0	6-P, 5, 1-M, 2-W, 10
P. secunda	18	1.6	......
Bromus anomalus	18	0.6	6-L, 6-S, 10
Weeds:			
Achillea lanulosa	37	0.7	6-P
Taraxacum officinale	27	8.0	......
Lathyrus leucanthus	24	1.2	6-S, 10
Viguiera multiflora	19	0.7	......
Galium boreale	18	0.1	10, 6-L
Browse:			
Symphoricarpos oreophilus	68	12.2	4, 6-P, 9, 10
Amelanchier alnifolia	43	13.4	......
Quercus utahensis	51	13.1	......
Artemisia tridentata	33	4.6	4, 9, 6-L
Mahonia repens	15	0.0	6-P

The browse-shrub type on the Eastern Slope is dominated by Gambel oak *(Quercus gambeli)*, true mountain mahogany, and skunkbush sumac *(Rhus trilobata)* either in mixture or occasionally in pure stands. In northern Colorado, true mountain mahogany is confined to rocky slopes in extensive stands. The line of demarkation between this type, so characteristic of the ridges or "hogbacks," and the mixed grassland composed of blue grama, bluestem wheatgrass, needleandthread, prairie junegrass, and threadleaf sedge which occurs on the deep soils of the longitudinal valleys between the slopes is so distinct as to appear artificial.

In central Colorado the browse-shrub type occurs as shrubby islands, dominated principally by Gambel oak, in the foothill grassland. In other localities the browse species commonly occur in scattered open stands with the above enumerated grasses forming the herbaceous understory.

The weeds of greatest frequency are hairy goldaster, common sunflower, and scarlet globemallow, all of which indicate unsatisfactory range conditions when they are abundant. Sunflowers or fringed sagebrush mark the locations of abandoned crop lands.

In western Colorado, the type aspect is generally determined by Utah white oak *(Quercus utahensis)* which occurs in dense stands (Fig. 17) or is mixed with mountain snowberry, Saskatoon serviceberry *(Amelanchier alnifolia)*, and big sagebrush. The latter three species also occur alone or in various combinations on slopes from which Utah oak is absent. The blue grama understory, typical of the type in eastern Colorado, is absent and in its place the most frequent species are sedges, prairie junegrass, Letterman needlegrass, bluestem wheatgrass, Sandberg bluegrass, nodding brome and other grasses. Kentucky bluegrass, as in other types, occurs most abundantly in the moist openings and along stream banks. Bluestem wheatgrass and slender wheatgrass *(Agropyron pauciflorum)* are occasionally abundant in the open park-like areas if moisture conditions are favorable.

FIG. 17. Oak type in southwestern Colorado. The overstory is so dense that relatively little forage is produced by herbaceous species.

Western yarrow, common dandelion, aspen peavine, showy goldeneye *(Viguiera multiflora)*, and northern bedstraw are representative of the weed species.

Dandelions frequently make up 80 percent or more of the herbaceous cover in the park areas of this type. A fair amount of forage is produced but a completely bare area may be left when the dandelions become dry and their leaves disintegrate with the advance of the season.

Oaks (*Quercus* spp.) are not important forage species although some use is made of them even under proper management (Forsling & Storm, 1929). Increase in density of the oaks and invasion of former grassland areas has greatly reduced the grazing capacity of the zones in which they occur. Eradication of oaks would be desirable in many instances if the cost were not prohibitive. Grazing practices which tend to prevent their further spread are the primary need at present.

ADDITIONAL SPECIES

GRASS AND GRASSLIKE

Agropyron pauciflorum
Bromus anomalus
B. carinatus
Carex geyeri
C. heliophila
Phleum pratense
Poa secunda
Sitanion hystrix
Stipa viridula

WEEDS

Arenaria fendleri
Artemisia gnaphalodes
Aster spp.
Erigeron spp.
Geranium spp.

Helianthus petiolaris
Lupinus spp.
Polygonum aviculare
Thalictrum fendleri
Thermopsis divaricarpa
Vicia americana

BROWSE
Cercocarpus ledifolius
Opuntia spp.
Prunus virginiana melanocarpa
Purshia tridentata
Ribes montigenum
Rosa woodsi fendleri

IMPORTANT SPECIES OF THE SEMI-DESERT AREA

The forage types of this area occur principally at elevations below 7,000 feet and in localities receiving an annual precipitation of less than 15 inches. The semi-desert areas occupy much of southwestern Wyoming (Vass & Lang 1938) and western and northwestern Colorado with an isolated island in south-central Colorado near Alamosa. These types are used primarily for winter grazing. The soils are largely alluvial and are characterized by varying amounts of alkali.

The sagebrush type occurs on soils that are moist to a considerable depth and that contain relatively small amounts of alkali. The saltbush types, which frequently alternate with or are interspersed in the sagebrush type are found on more alkaline areas where both drainage and water penetration are poor. The greasewood type occurs along the drainage channels where alkali salts have accumulated near the surface. It is the least productive of all the grazing types.

SAGEBRUSH TYPE

This type is best expressed in the Rocky Mountain region in northwestern Colorado and western Wyoming where it covers thousands of acres in which the only major variation is the occasional transition to saltbush or greasewood communities along the stream channels and in old lake beds. Big sagebrush is the most prominent and most abundant plant of this association. On areas which have not been severely overgrazed the sagebrush plants are usually spaced several feet apart and the intervening spaces are characterized by various grasses and weeds. Heavily used areas are frequently devoid of herbaceous vegetation and the sagebrush plants may grow in such dense stands as to present a closed cover. Severe overgrazing eventually results in the production of stunted clumps of sagebrush (Fig. 18), growing on pedestals, and excessive erosion of the soil between these clumps.

The commonest grasses of the type are thickspike wheatgrass *(Agropyron dasystachyum)* and Indian ricegrass (Table 21). The disappearance of these grasses or a reduction in their numbers to occasional clumps rapidly follows overutilization by grazing

FIG. 18. Sagebrush type heavily overgrazed by sheep for many years. Most of the grasses and forbs have disappeared.

animals. As early indication of overuse of these species is a decrease in vigor and numbers of the grasses between as compared with those within the sagebrush clumps. Bottlebrush squirreltail is typical of areas within the sagebrush type that are being depleted by grazing. It has little grazing value. Bluestem wheatgrass is sporadic in occurrence but furnishes good forage in the moist areas, particularly in early spring. In this type it may indicate soil disturbance due to excessive trampling.

TABLE 21. Important species of the sagebrush type.

Species	Frequency	Forage produced	Occurrence in other semi-desert types
Grass and grass-like species:	*Percent*	*Percent*	
Agropyron dasystachyum	67	12.0	13, 14
Oryzopsis hymenoides	52	7.1	13
Sitanion hystrix	12	0.5	......
Agropyron smithi	9	2.0	13
Weeds:			
Phlox hoodi glabrata	54	1.0	......
Arenaria hookeri	14	0.0	......
Actinea torreyana	13	0.0	......
Browse:			
Artemisia tridentata	97	30.1	14, 13
Chrysothamnus viscidiflorus pumulis	50	0.0	......
Eurotia lanata	38	11.0	13
Atriplex confertifolia	17	2.8	13,14
A. gardneri	10	1.9	13, 14

Native weeds which were formerly abundant have now disappeared from much of the type. Caespitose perennials such as smooth hoods phlox *(Phlox hoodi glabrata)* and low palatability species, Hooker sandwort *(Arenaria hookeri)* and rubberweed *(Actinea torreyana)*, typify the denuded spots at present. Tumbling Russian thistles occasionally form the only herbaceous cover in rainy seasons.

Various shrubs appear in mixture with big sagebrush depending on the intensity of grazing use and the soil type. In the more alkaline soils shadscale saltbush *(Atriplex confertifolia)* becomes dominant

and the sagebrush decreases in abundance. Gardner saltbush *(Atriplex gardneri)* occasionally invades the type on the heavier soils. Common winterfat *(Eurotia lanata)* when present is usually scattered and seldom occurs in appreciable density.

SECONDARY SPECIES

GRASS AND GRASSLIKE
Stipa comata

WEEDS
Eriogonum salinum
Gilia pungens
Salsola kali tenuifolia

BROWSE
Artemisia pedatifida
Grayia spinosa
Tedradymia spinosa

SALTBUSH TYPE

The saltbush type is one of the plant communities belonging to the northern desert shrub association (Stewart *et al.* 1940) and characterized by various species of Atriplex (Fig. 19). Variations in the frequency of occurrence and abundance of the various species justify separate lists of species for southwestern Colorado (Table 22) and for northwestern Colorado and western Wyoming (Table 23).

FIG. 19. Saltbush type in southern Wyoming showing Gardner saltbush in foreground and black greasewood in background.

Galleta is more abundant in southwestern Colorado than in the Red Desert of Wyoming. Indian ricegrass, thickspike wheatgrass, and bluestem wheatgrass are typical species but seldom occur in abundance. Grazing capacity is best determined on the basis of the shrubby species, particularly Gardner saltbush, shadscale saltbush, common winterfat, and bud sagebrush *(Artemisia spinescens)*. Greenmolly summercypress *(Kochia americana)* is not considered an important winter sheep feed in Colorado and Wyoming, owing to its low palatability and infrequent occurrence.

Various weed species occur in the saltbush type, of which the most frequent are tumbling Russian thistle, globemallow *(Sphaeralcea dissecta)*, seepweed *(Suaeda erecta)*, nodding eriogonum *(Eriogonum cernuum)*, and desert trumpet eriogonum *(E. inflatum)*.

SECONDARY SPECIES

GRASS AND GRASSLIKE
Aristida spp.
Bouteloua gracilis

WEEDS
Aplopappus sp.

BROWSE
Artemisia trifida
Opuntia spp.

TABLE 22. Important species of the saltbush type (southwestern Colorado).

Species	Frequency	Forage produced	Occurrence in other semi-desert types
Grass and grass-like species:	*Percent*	*Percent*	
Hilaria jamesi	68	26.5	......
Oryzopsis hymenoides	7	0.4	4
Weeds:			
Salsola kali tenuifolia	56	3.8	14
Sphaeralcea dissecta	18	0.0	......
Eriogonum spp.[1]	11	0.0	......
Browse:			
Atriplex confertifolia	65	36.7	14, 4
A. gardneri	34	13.6	14, 4
A. corrugata	26	13.4	......
Gutierrezia sarothrae	23	0.0	......
Eurotia lanata	12	1.7	4
Kochia americana	4	0.0	14

[1]Principally *Eriogonum cernuum* and *E. inflatum.*

TABLE 23. Important species of the saltbush type (northwestern Colorado and western Wyoming).

Species	Frequency	Forage produced	Occurrence in other semi-desert types
Grass and grass-like species:	*Percent*	*Percent*	
Oryzopsis hymenoides	20	1.8	4
Agropyron dasystachyum	12	1.5	4, 14
Hilaria jamesi	6	4.0	......
Agropyron smithi	7	1.7	4
Weeds:			
Salsola kali tenuifolia	15	1.0	14
Suaeda erecta	14	0.0	......
Browse:			
Atriplex gardneri	59	37.0	14, 4
A. confertifolia	39	22.5	14, 4
Eurotia lanata	31	18.2	4
Artemisia spinescens	28	2.3	14
A. tridentata	17	3.5	4, 14

GREASEWOOD TYPE

Black greasewood *(Sarcobatus vermiculatus)* is characteristic of heavy soils in which the alkali content exceeds 0.5 percent (Shantz 1938). Frequently it is the only plant found in the arid drainage courses and on the level alkaline valley floors (Fig. 20). It is sometimes considered to be a valuable range plant for both cattle and sheep for winter grazing. Poisoning and bloating of livestock, following utilization of this shrub, is occasionally reported.

FIG. 20. Greasewood type in southwestern Colorado. The impervious soil supports very little herbaceous vegetation.

In southern Colorado, particularly in the San Luis Valley, alkali sacaton *(Sporobolus airoides)*, inland saltgrass, blue grama, and mat muhly *(Muhlenbergia squarrosa)* are common associates of black greasewood (Table 24) and provide a desirable combination for winter grazing. When these grasses are present in fair density, management should be aimed at their perpetuation, and utilization of the browse species should be slight.

TABLE 24. Important species of the greasewood type (southern Colorado).

Species	Frequency	Forage produced	Occurrence in other semi-desert types
Grass and grass-like species:	*Percent*	*Percent*	
Sporobolus airoides	30	33.6	......
Distichlis stricta	38	15.3	......
Bouteloua gracilis	8	5.6	......
Muhlenbergia squarrosa	5	4.9	......
Weeds:			
Iva axillaris	4	0.0	......
Cardaria draba	7	0.0	......
Browse:			
Sarcobatus vermiculatus	67	32.8	......
Chrysothamnus spp.[1]	36	0.0	......
Kochia americana	10	0.1	13

[1]Principally *Chrysothamnus speciosus* and *C. lanceolatus.*

In western Colorado and western Wyoming, grasses are infrequent (Table 25), weeds are practically absent, and shrubby associates are more common. Gardner saltbush frequently forms the ground layer on level valley floors. Mixtures of black greasewood, shadscale saltbush, bud sagebrush, and big sagebrush occur in areas where the soil is less alkaline than it is where pure greasewood stands are found.

Unrestricted grazing in the greasewood type as in the other semi-desert types is evidenced by thinning of the naturally sparse plant cover, by disappearance of the grasses, and by dwarfing or killing of the browse species. Tumbling Russian thistle, poverty sumpweed, pepperweed whitetop *(Cardaria draba)*, and rabbitbrush are invading species which compete with the more desirable plants for the limited moisture supply.

TABLE 25. Important species of the greasewood type (western Colorado and western Wyoming).

Species	Frequency	Forage produced	Occurrence in other semi-desert types
Grass and grass-like species:	*Percent*	*Percent*	
Sporobolus airoides	10	1.1	......
Agropyron dasystachyum	7	1.7	4, 13
Weeds:			
Salsola kali tenuifolia	8	0.6	13
Browse:			
Sarcobatus vermiculatus	85	53.6	......
Atriplex gardneri	48	21.4	13, 4
Artemisia tridentata	26	5.2	4, 13
Atriplex confertifolia	16	5.7	13, 4
Artemisia spinescens	15	1.5	13
Kochia americana	11	0.1	13

SECONDARY SPECIES

GRASS AND GRASSLIKE	WEEDS
Agropyron smithi	*Stanleya* sp.
Carex filifolia	BROWSE
Hordeum jubatum	*Artemisia frigida*
Juncus spp.	*Artemisia pedatifida*
Muhlenbergia spp.	*Atriplex canescens*
Oryzopsis hymenoides	*Eurotia lanata*

DISCUSSION

Of the more than 2,000 species encountered in range surveys in Colorado and Wyoming, approximately 85 grass and grass-like plants, 130 weeds and 60 browse plants have been selected as important species from the range management standpoint. Most of these plants are important ecologically as well as economically; a considerable number of species of ecological importance, however, have been omitted in this classification, particularly those which are abundant in restricted localities and those which persist for relatively short periods of time on disturbed areas where succession is rapid as on abandoned plowed fields.

The total number of species selected as important plants represents approximately 14 percent of all species encountered. Of the total number encountered, about 7 percent are listed in tables along with their respective average frequencies and percentages of forage produced by range types. No particular significance is attached to the excess in number of weed or forb species over numbers of grass and grasslike or browse species. The number of browse species selected by the score card method is somewhat larger than might have been expected, probably because shrubs have been somewhat neglected in range management studies.

A comparison of the amount of forage produced by the major groups of species (grasses and grass-

like, weeds, and browse) reveals some marked differences between the various types and subtypes (Table 26). Grasses are the predominant forage producing species in the plains area, while browse is most important in the mountain types at lower altitudes and in the semi-desert area. The low percentage of forage contributed by grasses in the saltbush and greasewood types in northwestern Colorado and western Wyoming is attributed partly to the high alkaline content of the soils which tends to exclude many grasses and partly to the influence of unrestricted grazing in the past in many localities.

TABLE 26. Percentage of forage produced by plant groups in the different forage types and subtypes.

Type	Grass and grasslike	Weeds	Browse	Additional species
PLAINS AREA:				
Short-grass (E. Colorado)	94.6	2.5	0.1	2.8
Short-grass (E. Wyoming)	89.3	1.2	3.8	5.7
Dry Meadow	74.7	0.2	0.6	24.5
Sand Sagebrush	73.8	7.1	8.5	10.6
Big Sagebrush	80.0	1.1	12.7	6.2
Weed	75.0	16.2	0.0	8.8
MOUNTAIN AREA:				
Alpine and subalpine grassland	59.0	12.8	2.9	25.3
Spruce-fir	21.7	13.3	0.0	65.0
Lodgepole pine	18.7	9.5	8.1	63.7
Aspen	34.8	22.8	4.9	37.5
Ponderosa pine-Douglas fir	50.3	12.1	5.7	31.9
Ponderosa pine (S. Colorado)	77.6	0.2	3.4	18.8
Wet meadow	52.7	15.7	0.6	31.0
Park (higher altitudes)	16.1	33.1	4.2	46.6
Park (lower altitudes)	88.8	0.6	1.2	9.4
Sagebrush (higher altitudes)	19.3	23.8	25.4	31.5
Sagebrush (lower altitudes)	43.6	0.4	34.3	21.7
Pinon-juniper	71.4	1.2	23.4	4.0
Browse-shrub (E. Colorado)	62.4	6.0	21.7	9.9
Browse-shrub (W. Colorado)	19.0	3.5	43.3	34.2
SEMI-DESERT AREA:				
Sagebrush	21.6	1.0	45.8	31.6
Saltbush (SW Colorado)	26.9	3.8	65.4	3.9
Saltbush (NW Colorado and W. Wyoming)	9.0	1.0	83.5	6.5
Greasewood (S. Colorado)	59.4	0.0	32.9	7.7
Greasewood (W. Colorado and W. Wyoming)	2.8	0.6	87.5	9.1

The large amount of forage contributed by "additional species" (Table 26), or plants not listed in the tables for the spruce fir and lodgepole pine types, for example, is an indication of the diversity of the vegetation in these areas. Few individual species in the spruce fir type are of outstanding importance; more than 200 species must be included in the number required to make up 90 percent of the total available forage. In the short-grass type in eastern Colorado, on the other hand, blue grama and buffalograss contribute nearly 90 percent of all the forage produced.

Determination of the 10 or 12 most important species in each of the forage groups (grasses and grasslike, weeds, and browse) is difficult. In general the species listed in Table 27 have a high frequency of occurrence within the territory where they are found, are widely distributed in the two states as indicated by the number of types and subtypes in which they occur, and contribute more forage than the average. Species such as *Helenium hoopesi* and *Actinea richardsoni* have been included because their poisonous qualities result in severe livestock losses each year.

TABLE 27. A list of the most important species in Colorado and Wyoming.

Species	Average frequency	Average forage production	Occurrence in types and subtypes
Grasses and grasslike species:	*Percent*	*Percent*	*Total number*
Agropyron smithi	27	3.6	15
Bouteloua gracilis	64	51.5	14
Carex spp	31	5.4	20
Deschampsia caespitosa	31	17.2	3
Festuca arizonica	21	3.2	7
Hilaria jamesi	20	5.1	5
Koeleria cristata	25	1.2	14
Muhlenbergia montana	28	12.1	5
Oryzopsis hymenoides	31	3.7	9
Poa pratensis	15	4.8	8
Sporobolus spp	19	7.2	11
Stipa comata	24	2.4	8
Stipa lettermani	22	2.1	9
Weeds (forbs):			
Achillea lanulosa	27	1.6	11
Actinea richardsoni	18	0.0	6
Chenopodium album	27	1.0	6
Chrysopsis villosa	18	0.1	9
Erigeron spp	51	0.8	11
Helenium hoopesi	12	0.0	4
Potentilla spp	29	3.6	9
Salsola kali tenuifolia	27	2.6	12
Sphaeralcea coccinea	20	0.1	9
Taraxacum officinale	28	9.1	8
Vicia americana	26	0.8	6
Browse:			
Artemisia tridentata	61	14.9	12
Atriplex canescens	15	0.5	7
Atriplex gardneri	29	15.1	5
Cercocarpus montanus	12	4.5	6
Chrysothamnus spp	35	0.2	10
Eurotia lanata	31	10.9	10
Gutierrezia sarothrae	15	0.0	9
Opuntia spp	35	0.0	12
Purshia tridentata	10	1.0	5
Symphoricarpos oreophilus	32	6.0	6

Blue grama is the most important species in the two states. It has a high frequency, is an important forage species, and occurs over a wide territory. Its frequency varies from a low of 8 percent in the greasewood type of the semi-desert area of southern Colorado to a high of 94 percent in the short-grass plains of eastern Colorado. In localities where the frequency is low the plants are generally widely scattered and occur as individual tufts in contrast with the sod or turf form of growth on the plains. These differences in growth form, frequency, and the variations in density resulting from variations in soil type and precipitation account for wide variations in forage production from place to place. In the dry meadow type of the plains area blue grama has a relatively high frequency, 29 percent, but produces a low amount of forage in the type, 1.8 per-

cent. Field examination indicates that the individual plants are numerous but small and that they do not commonly develop a sod. It is also of interest that blue grama not only occurs in the semi-desert areas but appears to be increasing in abundance. Little information, however, is available on the effect of range management practices on the persistence or increase of blue grama in these arid types.

The species of widest occurrence is bluestem wheatgrass. It is exceeded in frequency, however, by several species. Its forage production is relatively low, partly as a result of sporadic occurrence in the types where it occurs and partly as a result of its occasional single stemmed habit of growth which results in small volume production.

In general, the meaning of the presence or absence and the condition of many of the other important plants which have been listed cannot be interpreted because of insufficient knowledge. They are in need of further study. Some of the lines of investigation of important species which would appear to be profitable include the following: indicator values; desirability or practicability of increasing certain plants in the forage cover; importance of weeds and browse in range management; the control of noxious and poisonous plants; and range utilization standards, designed to perpetuate the plants of highest forage value. The part that many species of high frequency play in secondary succession is little understood either from the ecological or range management viewpoint. Range recovery from a depleted or poor condition is essentially a process of secondary succession and as such deserves the attention of the ecologist.

It is hoped that the present paper will stimulate a more systematic and better choice of species for future studies in which ecological or range management principles are involved. Studies of vegetation in limited areas will necessarily require detailed examination of the flora. The generalized information gathered by many individuals and summarized here, however, should be an aid in orientation of species in local plant communities with the broader communities found throughout Colorado and Wyoming.

LITERATURE CITED

Baker, F. S. 1925. Aspen in the central Rocky Mountain region. U. S. Dept. Agr. Bul. **1291**. 46 pp.

Canfield, R. H. 1939. The effect of intensity and frequency of clipping on density and yield of black grama and tobosa grass. U. S. Dept. Agr. Tech. Bul. **681**. 32 pp.

Carpenter, J. Richard. 1940. The grassland biome. Ecol. Monog. **10:** 617-684.

Cassady, J. T. 1941. Management of sheep on summer range. The Nat. Woolgrower **31:** 19-20.

1941a. A method of determining range forage utilization by sheep. Jour. Forestry **39:** 667-671.

Clements, F. E. 1920. Plant indicators. Carnegie Inst. Wash. Pub. **290**.

1928. Plant succession and indicators. H. H. Wilson Co., New York City.

1935. Experimental ecology in public service. Ecology **16:** 342-363.

Clements, F. E., & E. S. Clements. 1941. Climate, climax, and conservation. Carnegie Inst. Wash. Yearbook **40**. Pp. 176-182.

Clements, F. E., & V. E. Shelford. 1939. Bio-ecology. John Wiley & Sons, Inc., New York City.

Cook, C. W. 1942. Insects and weather as they influence growth of cactus on the central Great Plains. Ecology **23:** 209-214.

Costello, D. F. 1941. Pricklypear control on short-grass range in the central Great Plains. U. S. Dept. Agr. Leaflet **210**.

1942. Maintaining short-grass ranges. Colo. State Col. Ext. Serv., Defense Bul. **D-33**. 12 pp.

1943. Returning abandoned cultivated lands to grazing will save short-grass range. Colo. Farm Bul. **5:** 15-17.

Costello, D. F., & Raymond Price. 1939. Weather and plant development data as determinants of grazing periods on mountain range. U. S. Dept. Agr. Tech. Bul. **686**. 31 pp.

Craddock, G. W., & C. L. Forsling. 1938. The influence of climate and grazing on spring-fall sheep range in southern Idaho. U. S. Dept. Agr. Tech. Bul. **600**. 43 pp.

Crafts, E. C. 1938. Height-volume distribution in range grasses. Jour. Forestry **36:** 1182-1185.

Doran, C. W. 1942. More profit with sheep on the range. West. Farm Life **44:** 3.

Forsling, C. L., & E. V. Storm. 1929. The utilization of browse forage as summer range for cattle in southwestern Utah. U. S. Dept. Agr. Cir. **62**. 29 pp.

Gordon, A., & A. W. Sampson. 1939. Composition of common California foothill plants as a factor in range management. Calif. Agr. Expt. Sta. Bul. **627**. 95 pp.

Interagency Range Survey Committee. 1937. Instructions for range surveys. (Mimeo.) 30 pp. (Available, U. S. Forest Service, Washington, D. C.)

Larson, Floyd. 1940. The role of the bison in maintaining the short-grass plains. Ecology **21:** 113-121.

Lommasson, Tom, & Chandler Jensen. 1938. Grass volume tables for determining range utilization. Sci. n.s. **87:** 444.

Marsh, C. D., A. B. Clawson, J. J. Couch, & H. Marsh. 1921. Western sneezeweed (Helenium hoopesii) as a poisonous plant. U. S. Dept. Agr. Bul. **947**. 46 pp.

McCreary, O. C. 1931. Wyoming forage plants and their chemical composition—studies No. 9. Wyo. Agr. Expt. Sta. Bul. **184**. 23 pp.

Merriam, C. Hart. 1892. The geographic distribution of life in North America with special reference to the Mammalia. Proceed. Biol. Soc. Wash. **7:** 1-64.

Packard, F. M. 1942. Wildlife and aspen in Rocky Mountain National Park, Colorado. Ecology **23:** 478-482.

Pechanec, J. F., & G. D. Pickford. 1937. A comparison of some methods used in determining percentage utilization of range grasses. Jour. Agr. Res. **54:** 753-765.

Ramaley, F. 1927. Colorado plant life. Univ. Colo., Boulder.

1939. Sand-hill vegetation of northeastern Colorado. Ecol. Monog. **9:** 1-51.

Sampson, A. W. 1919. Effect of grazing upon aspen reproduction. U. S. Dept. Agr. Bul. **741**.

1939. Plant indicators—concept and status. Bot. Rev. **5:** 155-206.

Sampson, A. W., & H. E. Malmsten. 1926. Grazing periods and forage production on the national forests. U. S. Dept. Agr. Bul. **1405.** 55 pp.

Sarvis, J. T. 1920. Composition and density of the native vegetation in the vicinity of the northern great plains field station. Jour. Agr. Res. **19:** 63-72.

Savage, D. A., & H. Everett Runyon. 1937. Natural revegetation of abandoned farm land in the central and southern great plains. Fourth Internatl. Grassland Cong. Pp. 178-182.

Shantz, H. L. 1911. Natural vegetation as an indicator of the capabilities of land for crop production in the great plains area. U. S. Dept. Agr. Bur. Plant Ind. Bul. **201.** 91 pp.

1917. Plant succession on abandoned roads in eastern Colorado. Jour. Ecology **5:** 19-42.

1938. Plants as soil indicators. Yearbook, U. S. Dept. Agr. Pp. 835-860.

Shreve, F. 1915. The vegetation of a desert mountain range as conditioned by climatic factors. Carnegie Inst. Wash. Pub. **217.** 112 pp.

Stewart, George, & S. S. Hutchings. 1936. The point-observation-plot (square-foot density) method of vegetation survey. Jour. Amer. Soc. Agron. **28:** 714-722.

Stewart, George, W. P. Cottam, & S. S. Hutchings. 1940. Influence of unrestricted grazing on northern salt desert plant associations in western Utah. Jour. Agr. Res. **60:** 289-316.

Stoddart, L. A. 1935. Range capacity determination. Ecology **16:** 531-533.

1941. Chemical composition of Symphoricarpos rotundifolius as influenced by soil, site, and date of collection. Jour. Agr. Res. **63:** 727-739.

Talbot, M. W. 1937. Indicators of southwestern range conditions. U. S. Dept. Agr. Farmers Bul. **1782.** 35 pp.

Tidestrom, Ivar. 1925. Flora of Utah and Nevada. Contrib. U. S. Nat. Herb. Vol. **25.** Washington, D. C.

Turner, G. T., & D. F. Costello. 1942. Ecological aspects of the pricklypear problem in eastern Colorado and Wyoming. Ecology **23:** 419-426.

U. S. Forest Service Region 4. 1939. Range utilization handbook. (Mimeo.) 61 pp.

U. S. Forest Service Region 5. 1939a. Range utilization handbook (offset printing). 51 pp.

Weaver, J. E., & F. W. Albertson. 1940. Deterioration of midwestern ranges. Ecology **21:** 216-236.

1942. History of the native vegetation of western Kansas during seven years of continuous drought. Ecol. Monog. **12:** 23-51.

Vass, A. F., & Robert Lang. 1938. Vegetative composition, density, grazing capacity and grazing land values in the Red Desert area. Wyo. Agr. Expt. Sta. Bul. **229.** 72 pp.